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Cover illustration: Photograph of Malabar Rose (*Pachliopta pandiyana* (Moore)) endemic to the Western Ghats, Kallar, Kerala, India. Photograp taken August 2004 by Krushnamegh Kunte, University of Texas at Austin, e-mail: krushnamegh@gmail.com.

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SPERM PRECEDENCE IN EXPERIMENTAL INTERSPECIFIC MULTIPLE MATINGS OF HYBRIDIZING NORTH AMERICAN TIGER SWALLOWTAIL BUTTERFLY SPECIES (LEPIDOPTERA: PAPILIONIDAE)

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ABSTRACT. *Papilio canadensis* and *P. glaucus* have multiply-mating females and males. Laboratory hand-pairings allowed us to by-pass natural mating preferences of polyandrous females and conduct sequential (twice-mated) lab pairings; one heterospecific and one conspecific male for each virgin female of *P. glaucus* or *P. canadensis*. Using electrophoresis and species-specific (diagnostic) allozymes, we were able to determine whether random fertilization (a mix of heterospecific sperm) or sperm precedence (either first or last male) existed for these twice-mated females. Since the number of useful double pairings for lab and field female analyses was low, we can only conclude that of double mated females, most are fertilized by males of their first mating, but that a mix of sperm and last male sperm precedence do occur at lower frequencies.

Overall, these lab results suggest that if it exists, sperm selection by females of *P. glaucus* and *P. canadensis* would not necessarily provide a clear mechanism of reproductive isolation. In fact, eggs from interspecific primary hybrid lab crosses (73 families of *Pg* × *Pc* and 17 families of *Pc* × *Pg* hybrids; all single pairing F_1 crosses) are as fertile and viable as those from parental types. The isolating mechanisms that maintained a narrow hybrid zone from 1980-1997 have not been sustained during the recent 1998-2003 period where extensive interspecific hybrid introgression and X-chromosome recombination has occurred. It is clear that even though lab-reared males were regularly fed a solution of honey water, amino acids, and electrolytes, they were less successful at producing larval offspring that were field-captured (wild) males when mated to virgin females. This difference in reproductive success mandates caution in extrapolation from lab to field studies. However lab-reared males can show first male or last male sperm precedence. It is also possible for a female to have a mixture of fertilizations from males of different species. We are therefore hesitant to interpret these preliminary results with relatively small sample sizes in the context of sexual selection theory. These results do complicate the interpretation of hybrid zone dynamics.

Additional key words: Conspecific sperm, *Papilio glaucus, P. canadensis,* polyandry, hybrid zone spermatophore..

INTRODUCTION

Females of many animal species mate multiple times within their fertile lifetime (Smith 1984; Birkhead and Møller 1998). There is evidence that these multiple matings may extend female life-span (Wagner *et al.* 2001), increase egg production (Wiklund *et al.* 1993; Boggs 1997a, 1997b, Karlsson 1998, Eady *et al.* 2000), and increase offspring viability (Lederhouse and Scriber 1987; Tregenza and Wedell 2002). It may also increase offspring weight/size (Sakaluk *et al.* 2002) or offspring reproductive success (Bernasconi and Keller 2001; Pai and Yan 2002). However, where males are of different species, egg production can be drastically reduced (Shapiro 2000) or post-zygotic hybrid offspring survival may be poor (Orr and Turelli 2001; Marshall *et al.* 2002). Mixtures of species diagnostic traits from a single mother could result from fertilization by both heterospecific and conspecific males in a hybrid zone. Clarification of sperm precedence for naturally hybridizing species is needed.

Sperm are stored for use in fertilization, sometimes for the entire life of the insect, in female organs called spermathecae (Cook and Wedell 1996; Gage 1998). Some species with different types of sperm storage organs (Pitnick *et al.* 1999) can separately store sperm from different males, as in the yellow dung fly (Ward 1998; Hellriegel and Bernasconi 2000). This creates the possibility that sperm from two (or more) different males are in competition for egg fertilizations, extending sexual selection beyond copulation. Packets of sperm (spermatophores) are transferred to polyandrous females of the North American tiger swallowtail butterfly species group, raising questions of sperm precedence and sperm competition from different mates.

Females of *Papilio glaucus* L. and *P. canadensis* R & J, often mate four to five times during their relatively short lifetime of three to six weeks (Lederhouse *et al.* 1989; Lederhouse 1995; Scriber *et al.* 1998a) and males can mate at least four times (Lederhouse 1995). We have shown that fertility declines in *P. glaucus* females after seven to eight days and that a second mating may restore it (Lederhouse and Scriber 1987; see also Watanabe 1988). This may be the result of sperm depletion or other factors.

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As in many Lepidoptera, these two species of *Papilio* usually package sperm in a spermatophore, which is energetically costly (Mann 1984; Watanabe and Hirota 1999). Sperm are often dependent upon the female's muscles to move them out of the spermatophore and transfer them to the spermatheca (Tschudi-Rein and Benz 1990). While the pattern of paternity in butterflies and moths is variable, it is believed that sperm from one male takes precedence. However, it might be an earlier mate instead of the most recent one that sires most or all of the offspring (Clarke and Sheppard 1962; Flint and Kressing 1968; Pair *et al.* 1977; Bissoondath and Wiklund 1997; Cook *et al.* 1997; Wedell and Cook 1998; LaMunyon 1999). The importance of which male's sperm sires offspring may be of even greater ecological significance when males are from different species, as can occur in hybrid zones of parapatric species.

Multiple-mating females and males of tiger swallowtail butterflies may encounter heterospecific mates as well as their conspecifics in the vicinity of hybrid zones such as the one across the Great Lakes region (generally at latitudes of 40-43°N) from Minnesota through Wisconsin, Michigan, New York State, and New England (Scriber 1996; Scriber *et al.* 2003). We have documented such parapatric range overlap and cases of natural hybridization of the species in the field (Luebke *et al.* 1988; Scriber 1990; Deering and Scriber 1998; Scriber *et al.* 1998b; Stump 2000; Ording 2001; Donovan and Scriber 2003; Hereau and Scriber 2003). Mating preferences of both *P. glaucus* and *P. canadensis* males in the field are both very strong for tethered *P. glaucus* females in 2-choice tests using size-matched, tethered virgin females, which represents a strong and unexpected asymmetry (Deering 1998; Deering and Scriber 2002). Females were capable of free flight on the thread tethers and were able to reject some male mating attempts. However, few rejections were observed for these lab-reared virgin females. No evidence of sex pheromones has been detected in field tests with cryptically caged virgin females compared to empty control cages behind dead display females (Deering 1998).

Interspecific hybridization for *P. glaucus* and *P. canadensis* has been documented to increase extensively within and north of the historical hybrid zone during the recent warming climatic trends during 1998–2003 (Scriber 2002a; Scriber and Ording 2005). The potential of post-mating (but prezygotic) reproductive isolation had not been examined for these butterflies (e.g. differential selection of sperm by females). In particular, we wondered whether multiple-mating females of *P. glaucus* or *P. canadensis* may cryptically select sperm of conspecifics over heterospecifics as suspected in grasshoppers (Hewitt *et al.* 1989; Bella *et al.* 1992), crickets (Gregory and Howard 1994; Howard *et al.* 1998), *Drosophila* (Price 1998), ladybird beetles (Katakura 1986b), and flour beetles (Wade *et al.* 1993). If so, strong conspecific sperm precedence could help explain why the hybrid zone has remained basically geographically distinct and ecologically stable for the past two centuries (Scriber *et al.* 1982, 1996) despite the capacity for strong flight and long range dispersal of both species (Scriber *et al.* 1998b).

We employed species-specific diagnostic allozymes to identify the paternity of larvae produced after two sequential hand pairings of individual virgin females with heterospecific and conspecific (or vice versa) males of *P. glaucus* and *P. canadensis*. We also compared males of the more distantly related *P. eurymedon*, *P. rutulus*, *P. multicaudatus*, and *P. troilus* (Hagen and Scriber 1991). The western species (*P. eurymedon*, *P. rutulus*, *P. multicaudatus)* also hybridize to various degrees (Sperling 1990, 2003; Scriber *et al.* 1995; Layberry *et al.* 1998; Guppy and Shepard 2001). Different benefits of multiple matings (accessory gland substances promoting increased egg production, ejaculates with nutritional benefits; Arnqvist and Nilsson 2000) may result from repeated mating with the same male versus different males (where indirect genetic benefits may also occur; Jennions and Petrie 2000; Zeh and Zeh 2001). The importance of comparing laboratory versus natural polyandrous matings (where females choose their mates and thus influence both the direct and indirect benefits; see Tregenza *et al.* 2003) has recently been emphasized for crickets (Sakaluk *et al.* 2002). Therefore, in addition to lab pairings with virgin females, wild allopatric females of *canadensis* and *glaucus* were captured and subsequently remated to heterospecific males after first collecting her field-fertilized (presumably conspecific) eggs for 1-3 days. Directional postcopulatory sexual selection (involving both sperm competition, where sperm from different males compete to fertilize eggs, and cryptic female choice, where females bias sperm use toward particular males) has been revealed by using artificial insemination in guppies to bypass the complications with natural mating preferences and mating order of polyandrous females (Evans *et al.* 2003). We have functionally accomplished the same thing with laboratory hand-pairing techniques for *Papilio*.

All female butterflies of the *P. glaucus* group are presumably polyandrous and store sperm in spermathecae . We hoped to determine whether sperm from either first or last males have precedence, whether the female may exert cryptic sexual selection of

conspecific sperm for fertilizing her eggs, or if a mixture of sperm from both species (with potential competition) was involved. In addition to being the first such study in these species, the implications of the results for hybrid zone dynamics and the interpretation of the genetics of offspring from wild-caught females could also be significant. From a single mother of hybrid zone origins, a mixture of odd segregating traits in offspring might be explained by multiple matings with males of different species (Clarke and Sheppard 1962).

METHODS

Pairings. All double pairings were conducted during the summers of 1996, 1997, and 1998 (Tables 1–4). Both wild-caught and lab-reared male and female butterflies were used for pairings. Females and males of *P. glaucus* (G) and *P. canadensis* (C) and males of *P. rutulus* (R), *P. eurymedon* (E), *P. multicaudatus* (M) were used. Lab-reared, newly eclosed, virgin females were hand-paired to males and allowed to oviposit in multichoice plastic arenas lined with host plant foliage as previously described (Scriber 1993). These were remated (after two to six days and having laid at least 20 eggs), again by hand pairing, to a male of a species different from that of the first male. Females were then allowed to oviposit again. Additionally, wild caught females were allowed to oviposit in plastic boxes, then remated after one to five days by hand-pairing to a male of a different species, and allowed to oviposit again. Only females that were actively laying eggs were remated. The duration of pairings was recorded, as transfer of spermatophores takes at least 30 minutes.

For the *P. glaucus* species group, larvae from eggs laid both before and after rematings were collected and reared on Wild Black Cherry (*Prunus serotina* Ehrh.), a common host of both *P. glaucus* and *P. canadensis*. Larvae of *P. troilus* were reared on *Sassafras albidum* Nutt. or *Lindera benzoin* (L.) Blume (Lauraceae). After reaching approximately the third instar, larvae were frozen at -80°C. Adults were frozen before or immediately after death. Females were later dissected to determine how many spermatophores were present at death. We include females that after dissection only had a single spermatophore (Tables 3 & 4), because we wanted to determine which of the two males passed it. However, we deleted these pairings in our summary of "last" (P2 = 1) or "first" (P2 = 0) sperm precedence. We are also aware that sperm transfer without leaving recognizable spermatophores can rarely occur in Lepidoptera (Cordero 1999). Analyses of egg fertility and viability of a set of single lab-paired females from 1996-1999 with no spermatophores (n=45) were compared to those with one present (n=274).

Female butterflies were fed a 20% honey solution and males were fed a 20% honey solution supplemented with amino acids and salts following Lederhouse *et al.* (1990). Lab-reared males were not paired until at least two days following adult eclosion. For comparison, various other single male pairings among these species were conducted (1996–1999). Comparisons of egg and larval offspring production from field-captured females for various species were also included from years 1983–2002. A separate group of primary (F_1) hybrid crosses between *P. canadensis* and *P. glaucus* from 1995–2002 were compared to the reproductive fitness of wild females of both species (Table 8) to provide a comparison of fecundity and viability.

Allozyme Electrophoresis. Electrophoresis was carried out on thin-layer cellulose acetate plates (Titan III, Helena Laboratories, Beaumont, TX), using methods of Hagen and Scriber (1991). Small larvae were homogenized whole in buffer while the head and thoraxes of larger larvae were homogenized in buffer. The distal half of the abdomen of adult males and the proximal half of the abdomen of adult females was used since the distal part of the female abdomen included male spermatophores. The enzyme 6-phosphate dehydrogenase (*Pgd*) was used to determine differences between the species of the *P. glaucus* species group since all 5 species are fixed for different diagnostic alleles (Hagen and Scriber 1991). Other enzymes with diagnostic differences between species were not used because those alleles were too faintly stained in larvae. Staining of *Pgd* was fainter for larvae than adults, but it was clear and interpretable. In other Lepidoptera, fixed allozyme differences have also been used to identify egg, larval, pupal, and adult species (Woods *et al.* 2001). Paternity of offspring produced after remating of our *Papilio* was established by determining alleles of *Pgd* allozymes of larvae produced after remating. In several cases, the males were lost (or accidentally not frozen soon enough) and could not be evaluated. Precedence for each female was expressed as P2, the proportion of larvae produced after the remating that were sired by the female's second mate.

RESULTS

Lab and wild pairings. Out of 82 interspecific double pairings for lab-reared females, only 32 produced larvae both before and after being remated (Table 1). The others either laid no eggs after being remated, laid no hatching eggs (all being either infertile or fertile and non-viable) after remating, or had laid no hatching eggs before being remated. Of the 32 females producing larvae both before and after being remated, five had been mated to males that shared allozymes.

Some interspecific introgression (or ancestral low-level polymorphisms, or residuals from earlier north/south Pleistocene hybrid zone movement) is found at the *Pgd* locus (Hagen and Scriber 1991; Scriber 1996; Scriber *et al.* 1998b) making the determination of paternity for offspring impossible in these cases, leaving 27 broods where P2 was determined. Of these females, 6 had only a single spermatophore recovered, and 3 others produced fewer than 5 larvae, leaving only 18 for P2 analyses. Since the sample sizes were so small, we did not conduct t-tests.

In addition to the sequential pairings of various lab-reared virgin females (Table 1), wild females were also set up in oviposition arenas and later remated to heterospecific males (Table 2). Out of 27 wild females, 20 produced larvae both before and after being remated. All of the remated wild females produced larvae before being mated. Only one female that had produced larvae after being remated had a P2 that was not possible to be determined electrophoretically, leaving 19 broods where P2 was determined (Table 2). Of these 19 females, 5 had only one (or no) spermatophores and another 7 had fewer than 5 larvae, leaving 7 for P2 allozyme analyses. A shared host plant (*Prunus serotina*) was used to minimize any differential mortality of larvae before the third instar samples for allozyme analysis, but this delay from egg hatch to the third instar, when allozyme samples were made, nonetheless may have introduced an unknown degree of selection bias due to differential mortality among genotypes. Larvae had allozymes corresponding to their parents in all of the cases where allozymes of parents (a once-mated female and her mate) were compared to larval offspring allozymes. We used *Pgd*, which is X-linked in *P. glaucus* and *P. canadensis*. Male homozygotes of *Pgd* could not be distinguished from female hemizygotes in larvae since the sex was not ascertained. The sample numbers are not high enough to be able to estimate accurately the actual population allele frequencies, but there is no reason to suspect non-Mendelian inheritance.

Of the 18 double-paired interspecific lab crosses examined, 11 showed first male sperm precedence (P2 = 0), 4 showed mixed parentage (P2 = 0.20 - 0.93), and 3 showed last male sperm precedence (P2 = 1). Only one of these three last male fertilizations was heterospecific in paternity (Table 3). Of the wild females remated to different species in the lab, 3 showed mixed parentage (from both males; P2 = 0.07-0.14) and the other 4 all showed first male sperm precedence (P2 = 0; Table 4). The number of useful double male pairings was insufficient to evaluate whether female selection of conspecific sperm was possible or not.

Durations of second pairings were recorded. No second pairings lasting less than 30 minutes resulted in sperm replacement. This is not surprising based on time needed for ejaculate transfer in other Lepidoptera (Watanabe and Sato 1993). However, most second pairings lasted for longer than 30 minutes and most females were found to be carrying two spermatophores (or more for wild caught females).

Singly-mated females illustrate the need for a minimum of 30 minutes of copulation duration for successful fertilization (Table 5). A surprisingly high number of females laid eggs even when no spermatophore was present (0.62, n = 45) compared to those with a spermatophore (0.75, n=274, Chi-square 3.32, n.s.). However, only a very small portion of matings with no spermatophores detected produced larvae (0.08, n=24) compared to those with a spermatophore (0.57, n=189, Chi-square 19.87, p< 0.001).

Even with regular feedings of males with a honey water/electrolyte "elixir" (as in Lederhouse *et al.* 1990), it is evident that lab-reared males are less successful at producing broods with larvae than are wild field-collected males (Table 6). An index of reproductive success also shows that primary F_1 interspecific hybrids between *P. glaucus* and *P. canadensis* parents (*Pc* × *Pg* and *Pg* × *Pc*) have offspring success that is intermediate compared to the parental types (Table 6).

Average hatchabilities of eggs (# larvae/total. eggs) from field-captured females of these 5 species (ranging from 0.43 to 0.70; Table 7) were comparable to our lab-reared virgin females in these experiments (0.25 to 0.72; Table 6). The proportions of females that oviposited ranged from 33% to 84% among the 7 *Papilio* species. The percentage producing larvae ranged from only 16% to 52% (Table 7). In a separate study of singly-mated females that did produce larvae (from 1995-2002), it was clear that the heterospecific hybrids between *P. glaucus* and *P. canadensis* were at no obvious selective disadvantage compared to the parental types; with mean egg viability of 68.0% (*Pc* × *Pg*) and 62.3% (*Pg* × *Pc*) compared with 58.9% for *P. canadensis* and 65.3% for *P. glaucus* (Table 8).

DISCUSSION

Sperm precedence. Second male precedence has been considered to be the rule in Lepidoptera (Drummond 1984), but our results showed 3 of 25 successful double interspecific matings complete second male sperm precedence (P2 = 1) in these tiger swallowtail butterflies (Tables 3 & 4). Two additional twice-mated females showed a large proportion of

TABLE 1. Types and number of double-paired *Papilio* females and reproductive success following remating. P2 is calculated as the proportion of larvae produced after a second mating that were sired by the female's second mate.

Double-pairing type (female × male 1 × male 2)	double-paired females	laying eggs after remating	producing larvae after remating	producing larvae before and after remating	producing larvae before and after remating where P2 could be determined
(C × C × G)	18	17	8	6	5
(C × G × C)	13	12	6	5	5
(G × G × C)	17	13	9	6	6
(G × C × G)	20	18	13	8	5
(C × C × E)	7	5	2	2	2
(C × E × C)	4	4	2	2	2
(G × G × M)	1	1	1	1	1
(G × M × G)	1	1	1	1	0
(G × R × G)	1	1	1	1	1
Total	82	72	43	32	27
		72/82 = 87.8	43/72 = 59.7	32/43 = 44.4	27/32= 84.4 %

C = *canadensis*, G = *glaucus*, M = *multicaudatus*, R = *rutulus*, E = *eurymedon*

TABLE 2. Types and number of remated wild-caught *Papilio* females and reproductive success following remating.

Double-pairing type (female wild × male)	Number remated wild-caught	Laying eggs after remating	Producing larvae after remating	Producing larvae before and after remating	Producing larvae before and after remating where P_2 could be determined
P. canadensis wild x *P. glaucus* (C wild × G)	8	7	6	6	6
(G wild × C)	2	2	2	2	2
(G wild ×E)	7	6	6	6	5
(G wild × M)	4	3	3	3	3
(G wild × R)	6	3	3	3	3
Total	27	21	20	20	19
		21/27 = 77.8	20/21 = 95.2	20/20 = 100	19/20 = 95%

E, M, R = *eurymedon*, *multicaudatus*, & *rutulus*, respectively

mixed sire offspring (P2 = 0.82 and 0.93) and 5 others showed less extensive mixing (P2 = 0.07-0.36). This pattern appears to be in contrast to the last mate sperm precedence believed to be typical of insects in general (Smith 1984) and especially Lepidoptera. All but one of the 20 Lepidoptera species studied have mean P2 values greater than 0.47 and most are greater than 0.60 (see Table 2.3 in Simmons 2001); although it is reported that distributions are bimodal with 0 or 1 values for most species. Lepidoptera having bimodal distributions create intermediate mean values of P2, and that is one reason why P2 analyses are not very useful in understanding mechanisms of sperm competition (Simmons and Siva-Jothy 2001). Last male sperm precedence occurred (at least partially) in only 10 of 25 double matings for which we could analyze diagnostic allozymes. However, offspring sired by the last male mate occurred in both *P. canadensis* and *P. glaucus* females even when this male was heterospecific (*canadensis*, *glaucus*, and *eurymedon*; Tables 3 & 4). In addition to these inconclusive results, the last male sperm precedence patterns in other insects is also known to break down when a third male is involved (Zeh and Zeh 1994) as is the case with many older *P. glaucus* and *P. canadensis* females (Lederhouse and Scriber 1987; Lederhouse *et al.* 1989; Lederhouse

TABLE 3. Last male sperm precedence , P2, the proportion of offspring that were sired by the second male, for double-paired lab-reared females. Also indicated are the number of larvae produced after remating that had paternity determined by electrophoresis (N), origin of the male used for remating, the days between pairings, the duration of the remating, and the number of spermatophores present in the female at death.

Type (female × male × male 2)	Male origin	Days between pairings	Duration of remating (minutes)	Spermatophores present	P2	N
C× C × G	lab	3	65	2	1	15
	lab	3	100	2	0	27
	lab	2	26	1	0	61
	lab	3	60	2	0.2	5
C × G × C	lab	3	59	2	0	7
	lab	3	35	1	0	22
	lab	2	>43	2	0	12
	wild	4	57	2	1	21
G × G × C	lab	5	93	1	0	16
	lab	2	>36	2	0	21
	lab	2	>38	2	0	23
	lab	3	62	2	0.36	11
	lab	3	63	2	0	26
	lab	3	106	1	0	14
G × C × G	lab	3	>30	2	0.82	11
	lab	4	85	2	0	72
	wild	2	87	2	0	26
	wild	4	>30	2	0	23
C × C × E	wild	4	>41	2	0	21
	wild	2	73	2	0.93	14
C × E × C	wild	2	>85	1	0	21
	wild	2	>91	2	1	5
G ×R × G	wild	1	99	2	0	19

1995).

The relatively high success of first matings compared to the second matings in our studies is due to unknown factors. One possibility is simply that we did not wait long enough after the first pairing for natural decline in fertility or sperm volume before the second mating was made. For example, Lederhouse and Scriber (1987) have shown that fertility of these species declines over the first week after mating, but that the decline is most rapid after 6–10 days for *P. glaucus* and after 4–7 days for *P. canadensis*. Females in the field may normally reject second males for a longer period of their life than was the case for our experimentally forced laboratory hand pairings. It is also possible that the second male's sperm may have had insufficient time to reach the spermatheca of females in 2–3 days. Another area that deserves additional experimentation would be the assessment of whether males prevented from their

TABLE 4. Sperm precedence P2 for remated wild-caught females. Also indicated are the number of larvae produced after remating that had paternity determined be electrophoresis (N), origin of the male used for remating, the days between collection of the female and remating, the duration of the remating, and the number of spermatophores present in the female at death.

Type(female wild × male)	Male origin	Days until remating	Duration of remating (minutes)	Spermatophores present	P2	N
C wild × G	wild	3	43	2	0	7
	wild	4	33		0	14
	wild	3	60	3	0.14	7
	wild	3	72	3	0	5
G wild × C	lab	2	42	1	0	20
	lab	2	49	2	0	20
G wild × E	wild	1	>40	4	0.07	14
	wild	1	54	2	0.12	8
	wild	4	64	1	0	22
	wild	4	>75	2	0	21
G wild × R	wild	1	27	1	0	11

natural choice of female mates (in hand-paired cases) would withhold or reduce the amount of sperm transferred in laboratory pairings compared to natural matings. Few studies exist of sperm utilization patterns in nature (Cobs 1977; Allen *et al.* 1994; LaMunyon 1994). However, recent research shows that male ejaculate expenditures are dynamic and that males assess the mating status and relative fecundity of females and subsequently modulate the quantity or quality of ejaculate they pass to females (Wedell *et al.* 2002). This also exists as a possible explanation of our poor second mating success.

The roles of apyrene (lacking a nucleus) and eupyrene (with nucleus) sperm in competition (Cook and Wedell 1996, 1999; Watanabe *et al.* 2000) are completely unknown for these two *Papilio* species, and knowing these might help clarify results such as ours. The degree of polygamy and polyandry will vary with age, extent of protandry, the size of spermatophores, as well as species characteristics, all of which makes understanding sperm precedence a complex venture with slowed progress (Kempanaers *et al.* 2000; Pitnick and Brown 2000; Wiklund 2003).

The females that continued to produce fertile eggs and larvae sired by an earlier male (70% of those shown in Tables 3 and 4) also did so even when this original mate was a heterospecific male (followed in mating sequence by a conspecific male). This further suggests that these *Papilio* females may not be exerting active or passive conspecific sperm selection (Birkhead 2000). It has been suggested that genetic benefits from mate choice may be context-specific (Qvarnström 2001). In any case, it is feasible that sperm competition could override any cryptic female selection should it be found to occur.

The failure of many second matings to sire offspring in these interspecific pairing sequences is likely due to some of the same problems encountered in first pairings (Stump 2000). For example, as with first pairings, it appears that second pairings lasting at least 30 minutes are required for sperm replacement (Table 3). We found in *Papilio* single mating studies (Table 6) that only about 25-45% of hand pairings gave rise to some larvae (24.0% *canadensis* × *canadensis*, n=75; 32.4% *glaucus* × *glaucus*, n=33; 42.1% of *glaucus* x *canadensis* hybrids, n=38; and 44.0% of *canadensis* × *glaucus* hybrids, n=50: Stump 2000). Previous studies showed that in 1986 only 19% of 75 pairings produced some larvae (14 fertile females averaging 27 larvae from 73 eggs) After feeding males an elixir solution of amino acids, electrolytes, and sugar our results improved to 90% of 20 females producing some larvae (18 fertile females averaging 44 larvae from 105 eggs; Lederhouse *et al.* 1990).

We do not know the explanation for seemingly low percentages of mating success, but it is reasonable to assume that similar problems may explain at least a portion of the low second mating "replacement" success (70% of females continued to use earlier sperm). Wild

TABLE 5. Success of single mate pairings as indicated by those with viable larvae, grouped by mating duration. The pairings[1] were of various types (conspecific, heterospecific, backcross, and F_2), involved various *Papilio* species (*P. canadensis, P. glaucus, P. eurymedon, P. rutulus, P. multicaudatus, and P. troilus*), and were between lab-reared virgin females and either lab-reared or wild-caught males. Sample sizes for each duration/category are indicated in parentheses. Not all females were dissected and examined for a spermatophore.

Duration (minutes)	Proportion of pairings with a spermatophore[2]		Proportion of all pairings producing eggs		Proportion of pairings with larvae (of those with eggs)	
<30	0.0	0 / 10	61.1	11 / 18	0.0	0 / 11
30-90	94.6	210 / 222	75.3	223 / 296	59.2	132 / 223
>90	76.7	23 / 30	78.7	37 / 47	56.8	21 / 37

[1]all 1996-1999 laboratory hand-pairings of various *Papilio* populations or species were included.
[2] Some females were not examined for spermatophores

females of the 7 species also had low proportions successfully ovipositing and producing larvae (Table 7). Rather than sperm competition, our experimental procedures (second matings after only 2–6 days) may be a partial explanation for our generally low second male fertilization success. Waiting 7–8 days might better reflect the natural remating behavior and physiological. needs of females. Remating interval and spermatophore size can also affect the P2 values and number of matings for Lepidoptera (Drummond 1984; Lederhouse *et al.* 1989; Simmons and Siva-Jothy 2001).

First or last male sperm precedence may occur and be operational in different ways for multiple matings and be limited to only conspecific males (or only heterospecific males). In other species, viability of offspring has been shown to increase with additional conspecific male mates by avoiding the costs of inbreeding (Tregenza and Wedell 2002) or by gaining other genetic benefits (Yasai 1998; Newcomer *et al.* 1999; Jennions and Petrie 2000; Zeh and Zeh 2001; Sakaluk *et al.* 2002). Our experiments involved only combinations that used male mates from two different species. No double conspecific matings were made in this study. With hand-pairings, females were unable to make natural mate choices seen for females with free choice either in the lab or in the field (which can also vary; Sadek 2001).

Males of various insect species may attempt to guard their mates from competing males (Birkhead and Parker 1997) or to secrete mating plugs to block competitors access to the female's reproductive tract (Thornhill and Alcock 1983; Orr 1995). In addition, males may attempt to gain an advantage over potentially competing sperm by a number of mechanisms. First, there may be removal of previous male sperm (Lefevre and Jonsson 1962; Waage 1979; Ono *et al.* 1989; Orr 1995; Price *et al.* 2001). Secondly, hindering or rendering rival sperm non-functional with seminal secretions may occur (Katakura 1986a; Katakura and Sobu 1986; Harshman and Prout 1994; Clarke *et al.*

TABLE 6. Index of mating success for single mate pairs (1996-1999). For each pairing type, this is calculated as the proportion of pairings producing hatching larvae multiplied by the average hatchability of broods producing larvae. Female listed first in each pairing type.

Pairing Type (Female × Male) origin	(n)	Of pairings lasting at least 30 minutes, proportion producing larvae	Average egg hatchability of pairings producing larvae	Index of mating success
C ×C wild	(17)	0.45	0.49 ± 0.06	0.22
C × C lab	(7)	0.11	0.40 ± 0.12	0.04
G × G wild	(18)	0.78	0.72 ± 0.13	0.43
G × G lab	(18)	0.42	0.63 ± 0.07	0.26
C × G wild	(22)	0.52	0.61 ± 0.06	0.32
C × G lab	(10)	0.33	0.47 ± 0.10	0.16
G × C wild	(37)	0.59	0.66 ± 0.04	0.39
G × C lab	(4)	0.20	0.28 ± 0.09	0.06
T × G wild	(6)	0.67	0.25 ± 0.03	0.17
(C × G) × C wild	(17)	0.52	0.37 ± 0.06	0.19

(C × G) × C are backcross broods using hybrid females and wild *canadensis* males.
T = *P. troilus*

TABLE 7. Pooled total laboratory lifetime egg and larval production of wild field-collected *Papilio* females of the tiger swallowtail (*glaucus*) species group.

	Female Families			Population traits		
Species	**Total (n)**	**with Eggs**	**with Larvae**	**Total eggs**	**total larvae**	**hatchability (l/e)**
canadensis	730	353 (48%)	230 (32%)	13205	6311	.478
glaucus	959	524 (55%)	369 (38%)	31806	17341	.545
rutulus	65	43 (66%)	33 (51%)	1479	795	.538
eurymedon	33	11 (33%)	5 (16%)	297	172	.579
multicaudatus	25	21 (84%)	13 (52%)	599	259	.431
alexiares	31	19 (61%)	12 (38%)	919	475	.517
troilus	88	55 (63%)	35 (39%)	4417	3083	.698

P. canadensis and *P. glaucus* (and *P. alexiares*) data are from 1983-1986 only (others all include 1991-2002 individuals as well as 1983-1986).

1995; Rice 1996; Price *et al.* 1999, 2000). Thirdly, diluting or delaying competing sperm with sperm of higher volumes may be used (Sugawara 1979; Dickinson 1986; Gage and Baker 1991; Karlsson 1995; Gage and Barnard 1996; Simmons and Siva-Jothy 1998). Fourthly, transferring sperm or spermatophores of higher quality or effectiveness may give an advantage (Bertran *et al.* 1996; Smedley and Eisner 1996; Vahed 1998; LaMunyon and Ward 1999; Gilchrist and Partridge 2000; Stjernholm and Karlsson 2000; Price *et al.* 2001; Bergstrom and Wiklund 2002). Finally, there may be production of high volumes of non-nucleated apyrene sperm, which may prevent fertilization by eupyrene sperm of former males (Silberglied *et al.* 1984; Watanabe *et al* 2000). However, since some females may potentially manipulate sperm storage and use (Birkhead *et al.* 1993; Sakaluk and Eggert 1996; Siva-Jothy and Hooper 1996; Otronen 1997; Wilson *et al.* 1997; Neubaum and Wolfner 1999; Olsson *et al.* 1999) to give certain types of sperm a potential competitive advantage (e.g. to conspecific males over heterospecific males) (Robinson *et al.* 1994; Albuquerque *et al.* 1996; Eberhardt 1996; Howard 1999), the particular mechanisms determining which sperm wins is difficult to discern. It may relate to the nature of seminal fluids (Price 1997; Simmons 2001) or of the deposition patterns in all female storage components (Ward 1993). Also, both male and female processes may interact to produce sperm displacement or to affect the outcome of sperm competition (Clark *et al.* 1999; Simmons *et al* 1999; Eberhard 2000; Ward 2000; Simmons 2001). However, males attempting to increase their own fertilization success can result in a decrease of female fitness, producing sexual conflict (Stockley 1997; Simmons 2001; Chapman *et al.* 2003; Pizzari and Snook 2003). At a local population level, such male-female conflict within a species can lead to the rapid evolution of reproductive isolation (Tregenza 2003; Martin & Hosken 2003). The role such sexual selection may have in the reproductive isolation of hybridizing species such as these *Papilio* is currently unknown but may be extensive. Our study is only preliminary, and was conducted to assess the physiological possibilities of differential sperm use by multiply mated females and to see if consistent patterns of sperm precedence occurs. In these lab studies, we were unable to test sexual selection theory.

CONCLUSIONS

We have shown that, under our sequential double mating regime, females of *P. glaucus* and *P. canadensis* generally produce larvae fertilized by the first rather than second male. Sperm mixing (with eggs fertilized by both species) and last male sperm precedence do occur at lower frequencies than first male sperm precedence. However, we had insufficient numbers of useful two-species matings of our lab and wild females to evaluate any potential conspecific cryptic sexual selection of the sperm types by females. Since it is so difficult to distinguish selection from sperm competition, it remains controversial (Simmons and Siva-Jothy 2001) whether females really have some influence or selection-capability in cases with conspecific sperm precedence (Howard 1999). However, the poorly understood role of sperm from different species in reproductive isolation in *Papilio* or other hybrid zones for polyandrous females may be significant (Arnold 1997; Endler 1998; Turelli *et al.* 2001; Howard *et al.* 2002; Via 2002; Andolfatto *et al.* 2003). It was evident in these studies that lab-reared males (even when fed an amino acid, salt, sugar elixir solution; as in Lederhouse *et al.* 1990) were still inferior to field-collected "wild"

TABLE 8. Egg viability for wild *Papilio glaucus*, wild *P. canadensis*, their reciprocal hybrids (females lab reared; males wild). Data represent the mean (± se) of all individual females (1995–2002).

	(# of females)	Total larvae	Total eggs	Egg Viability
P. glaucus	(246)	77.3 (5.1)	110.5 (5.7)	65.3 (1.6)%
P. canadensis	(305)	31.7 (2.3)	53.5 (2.9)	58.9 (1.7)%
Primary Hybrids				
Pg × Pc	(73)	108.5 (11.1)	167.1 (15.1)	62.3 (3.6)%
Pc × Pg	(17)	55.2 (13.0)	77.1 (16.6)	68.0 (6.2)%
Backcrosses (1997-2002);				
PgPc × Pc	(3)	118.0 (37.3)	148.3 (42.9)	78.5 (3.3) %
PcPg ×Pg	(6)	18.6 (9.9)	33.2 (10.8)	44.9 (12.2) %
PcPg × Pc	(20)	33.2 (7.0)	80.1 (10.9)	39.9 (5.6) %
Pg × PgPc	(1)	278	288	96.5 %
Pg × PcPg	(1)	17	143	12.0 %
F_2 Hybrids				
PcPg × PcPg	(2)	24.5	80.1	16.9 %
PgPc × PgPc	(1)	12	63	19.1 %

Papilio glaucus from populations in various states of the USA (FL, GA, OH, MD, VA, MO, MI)
P. canadensis from various populations in Canada and the USA (AK, WI, MI, NY, VT)
T-tests between *P. glaucus* vs. *P. canadensis* were all significant ($p < 0.01$) for total larvae, total. eggs, and egg viability. For hybrids (*Pg x Pc* vs. *Pc x Pg*) viabilities were not significantly different, but total eggs and total larvae were ($p < 0.01$). Mean egg viability of Backcross type *PcPg x Pc* (39.9%, n=20 families) was significantly lower than both parental types and both primary hybrids (all $p < 0.001$). Another two backcross types (n=6; and n=20 families) were not significantly different than parentals and primary hybrids for egg viability (genotypes with only 1 or 2 families were not compared).

males with respect to reproductive potential in hand-pairings for these *Papilio*. Differential larval food quality and natural puddling behavior of adult males (Pivnick and McNeil 1987; Boggs 1997a, 1997b) can affect male physiological virility and mating success and may largely account for the higher reproductive success of wild males than lab-reared males in our study.

Finally, the extent of hybrid vigor as seen in our F_1 hand-paired lab crosses (see also Donovan 2001; Scriber *et al.* 2003) may not occur in the natural field situation where hybrid males (Davies 1997) or natural enemies might differentially affect the fitness of hybrids (e.g. Mallet and Barton 1989) or backcrosses (Hagen and Scriber 1995; Dasmahaptra *et al.* 2002; Presgraves 2002). Recent examples of likely recombinant hybrid speciation in insects (Schwarz *et al.* 2005; Scriber and Ording 2005; see also Rieseberg *et al.* 2001) depend on introgressive hybridization. However, the role of sperm precedence in the recently apparent ineffectiveness of prezygotic barriers between *P. glaucus* and *P. canadensis* (Deering and Scriber 2002; Scriber 2002a; Donovan and Scriber 2003; Scriber *et al.* 2006) was not resolved by this study.

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LITERATURE CITED

ALBUQUERQUE, G. S., C. A. TAUBER & M. J. TAUBER. 1996. Post-mating reproductive isolation between *Chrysopa quadripunctata* and *Chrysopa slonnae*: mechanisms and geographic variation. Evolution 50:1598–1606.

ALLEN, G.R., D. J. KAZMER & R. F. LUCK. 1994. Post-copulatory male behavior, sperm precedence and multiple mating in a solitary parasitoid wasp. Anim. Behav. 48: 635–644.

ANDOLFATTO, P.,J.M. SCRIBER & B. CHARLESWORTH. 2003. No association between mitochondrial DNA haplotypes and a female-limited mimicry phenotype in *Papilio glaucus*. Evolution 57: 305–316.

ARNOLD, M. L. 1997. Natural Hybridization and Evolution. Oxford Univ. NY.

BELLA, J. L., R. K. BUTLIN, C. FERRIS & G. M. HEWITT. 1992. Asymmetrical homogeny and unequal sex ratio from reciprocal mating-order crosses between *Chorthippus parallelus* subspecies.

Heredity 68:345–352.
BERGSTROM, J. & C. WIKLUND. 2002. Effects of size and nuptial gifts on butterfly reproduction: can females compensate for a smaller size through male-derived nutrients? Behav. Ecol. & Sociobiol. 52: 296–302.
BERNASCONI, G. & L. KELLER. 2001. Female polyandry affects their sons' reproductive success in the red flour beetle *Tribolium castaneum*. J. Evol. Biol. 14:186–193.
BERTRAM, M. J., D. M. NEUBAUM, & M. F. WOLFNER. 1996. Localization of the *Drosophila* male accessory gland protein ACP36DE in mated female suggests a role in sperm storage. Insect Biochem. Mol. Bio. 261:971–980.
BIRKHEAD, T. R. 1998. Cryptic female choice: criteria for establishing female sperm choice. Evolution 52:1212–1218.
——. 2000. Defining and demonstrating postcopulatory female choice again. Evolution 54:1057–1060.
BIRKHEAD, T. R. & G. A. PARKER. 1997. Sperm competition and mating systems, pp. 121–145. *In* Krebs, J. R., N. B. Davies (eds.) Behavioral Ecology. Oxford, Blackwell Scientific.
BIRKHEAD, T. R., A. P. MOLLER & W. J. S. SUTHERLAND. 1993. Why do females make it so difficult for males to fertilize their eggs? J. Theoretical Biol. 161:51–60.
——. 1998. Sperm competition and sexual selection. San Diego: Academic Press.
BISSOONDATH, C. J. & C. WIKLUND. 1997. Effect of male body size on sperm precedence in the polyandrous butterfly, *Pieris napi* L. (Lepidoptera: Pieridae). Behav. Ecol. 8:518–523.
BOGGS, C. L. 1997a. Reproductive allocation from reserves and income in butterfly species with differing adult diets. Ecology 78: 181–191.
BOGGS, C. L.. 1997b. Dynamics of reproductive allocation from juvenile and adult feeding: radiotracer studies. Ecology 78: 192–202.
CHAPMAN, T., L. F. LIDDLE, J. M. KALB, M. F. WOLFNER, & L. PARTRIDGE. 1995. Cost of mating in *Drosophila melanogaster* females is mediated by male accessory gland products. Nature 373:241–244.
CHAPMAN, T., G. ARNQVIST, J. BANGHAM & L. ROWE. 2003. Sexual conflict. Trends Ecol. Evol. 18:41–47
CLARK, A. G., M. AGUADÉ, T. PROUT, L. G. HARSHMAN & C. H. LANGLEY. 1995. Variation in sperm displacement and its association with accessory gland protein loci in *Drosophila melanogaster*. Genetics 139:189–201.
CLARK, A. G., D. J. BEGUN & T. PROUT. 1999. Female X male interactions in *Drosophila* sperm competition. Science 283:212–220.
CLARK, C. A. & P. M. SHEPPARD. 1962. Offspring from double matings in the swallowtail butterflies. Entomologist. August:199–202.
COBBS, G. 1977. Multiple insemination and male sexual selection in natural populations of *Drosophila pseudoobscura*. Amer. Natur. 111: 641–656.
COOK, P. A. & N. WEDELL. 1996. Ejaculate dynamics in butterflies: a strategy for maximizing fertilization success. Proc. Roy. Soc. London, Series B 263:1047–1051.
——. 1999. Non-fertile sperm delay female remating. Nature 397:486.
COOK, P. A., I. F. HARVEY & G. A. PARKER. 1997. Predicting variation in sperm precedence. Philosophical Transactions of the Royal. Society of London, Series B. 352:771–780.
CORDERO, C. 1999. Is spermatophore number a good measure of mating frequency in female *Callophrys xami* (Lycaenidae)? J. Lepid. Soc. 53:169–170.
COYNE J. A. & H.A. ORR (2004) Speciation. Sinauer, Sunderland, MA, 545 pp.
DASMAHAPATRA, K.K., M.J. BLUM, A. AIELLO, S. HACKWELL, N. DAVIES, E.P. BERMINGHAM, & J. MALLET. 2002. Inferences from a rapidly moving hybrid zone. Evolution 56: 741–753.
DAVIES, N., A. AIELLO, J. MALLET, A. POMIANKOWSKI & R. E. SILBERGLIED. 1997. Speciation in two neotropical butterflies: extending Haldane's rule. Proc. Roy. Soc. London B 264: 845–851.
DEERING, M. D. 1998. Preferential. mate selection by males as a reproductive isolating mechanism between the swallowtail species. *Papilio glaucus* and *P. canadensis* (Lepidoptera: Papilionidae). M.S. Thesis. Michigan State University, East Lansing, Michigan.
DEERING, M. D. & J. M. SCRIBER. 1998. Heterospecific mating behavior of *Papilio palamedes* in Florida (Lepidoptera: Papilionidae). Holarc. Lepid. 5:49–51.
——. 2002. Field bioassays show heterospecific mating preference asymmetry between hybridizing North American *Papilio* butterfly species (Lepidoptera: Papilionidae). J. Ethology 20:25–33.
DICKINSON, J. L. 1986. Prolonged mating in the milkweed leaf beetle *Labidomera clivicollis clivicollis* (Coleoptera: Chrysomelidae): a test of the "sperm loading" hypothesis. Behavioral Ecol. Sociobiol. 18: 331–338.
DONOVAN, J. 2001. Are hybrids more fit than their parental types? A test using two swallowtail butterfly species, *Papilio glaucus* and *P. canadensis* (Lepidoptera: Papilionidae) MS Thesis. Michigan State University. East Lansing, MI. 79pp.
DONOVAN, J. & J. M. SCRIBER. 2003. Detection and verification of a natural. primary hybridization event between two Tiger Swallowtail Butterfly species in northern Michigan. J. Lepid. Soc. 57:25–35.
DRUMMOND, B. A. 1984. Multiple mating and sperm competition in the Lepidoptera, pp. 290–370. In Smith, R. L. (ed.), Sperm competition and the evolution of animal mating systems. Academic Press, New York.
EADY, P. E., N. WILSON & M. JACKSON. 2000. Copulating with multiple males enhances female fecundity but not egg-to-adult survival in the bruchid beetle, *Callosobruchus maculatus*. Evolution 54:2161–2165.
EBERHARD, W. G. 1996. Female control: sexual selection by cryptic female choice. Princeton University Press, Princeton, New York, pp 501.
——. 2000. Criteria for demonstrating post-copulatory female choice. Evolution 54:1047–1050.
ENDLER, J. 1998. The place of hybridization in evolution. Evolution 52: 640–644.
EVANS, J. P., L. ZANE, S. FRANCESCATO, & A. PILASTRO. 2003. Directional postcopulatory sexual. selection revealed by artificial insemination. Nature 421:360–363.
FLINT, H. M. & E. L. KRESSIN. 1968. Gamma irradiation of the tobacco budworm: sterilization, competitiveness, and observations on reproductive biology. J. Econ. Ent. 61:478–483.
GACK, C. & K. PESCHEK. 1994. Spermathecal morphology, sperm transfer and a novel mechanism of sperm displacement in the rove beetle, *Aleochara curtula* (Coleoptera: Staphylinidae). Zoomorphology. 114:227–237.
GAGE, A. R. & C. J. BARNARD. 1996. Male crickets increase sperm number in relation to competition and female size. Behav. Biol. Sociobio. 38:349–353.
GAGE, M. J. G. 1998. Influences of sex, size, and symmetry on ejaculate expenditure in a moth. Behav. Ecol. 9:592–597.
GAGE, M. J. G. & R. R. BAKER. 1991. Ejaculate size varies with sociosexual situation in an insect. Ecol. Ent. 16:331–337.
GILCRIST, A. S. & L. PARTRIDGE. 2000. Why is it different to model sperm displacement in *Drosophila melanogaster*: the relation between sperm transfer and copulation duration. Evolution. 54:534–542.
GREGORY, P. G. & D. J. HOWARD. 1994. A post-insemination barrier to fertilization isolates two closely related ground crickets. Evolution. 48:705–710.
GUPPY, C. S. & J. H. SHEPARD. 2001. Butterflies of British Columbia. UBC Press, Vancouver, BC.
HAGEN, R. H. & J. M. SCRIBER. 1991. Systematics of the *Papilio glaucus* and *P. troilus* groups (Lepidoptera: Papilionidae): inferences from allozymes. Ann. Ent. Soc. Amer. 94:380–395.
——1995. Sex chromosomes and speciation in the *Papilio glaucus* group, pp.211–228. *In* Scriber, J.M., Y. Tsubaki, R. C. Lederhouse (eds.), Swallowtail butterflies: their ecology and evolutionary biology. Scientific Publishers, Gainseville, Florida.

HARSHMAN, L. G. & T. PROUT. 1994. Sperm displacement without sperm transfer in *Drosophila melanogaster*. Evolution 48:758–766.

HELLRIEGEL, B. & G. BERNASCONI. 2000. Female-mediated differential sperm storage in a fly with complex spermathecae, *Scatophaga stercoraria*. Animal Behav. 58:311–317.

HEREAU, H. & J. M. SCRIBER. 2003. Interspecific copulation of a dark morph *Papilio glaucus* female and a male *P. polyxenes* (Lepidoptera: Papilionidae). J. Lepid. Soc. 57:71–74

HEWITT, G. M., P. MASON, & R. A. NICHOLS. 1989. Sperm precedence and homogamy across a hybrid zone in the alpine grasshopper *Podisma pedestris*. Heredity 62:343–353.

HOWARD, D. J. 1999. Conspecific sperm and pollen precedence and speciation. Ann. Rev. Ecol. Syst. 30:109–132.

HOWARD, D. J., P. G. GREGORY, J. CHU & M. L. CAIN. 1998. Conspecific sperm precedence is an effective barrier to hybridization between closely related species. Evolution 52:511–516.

HOWARD, D.J., J. L. MARSHAL.L, D. D. HAMPTON, S. C. BRITCH, M. L. DRANEY, J. CHU & R. G. CANTRELL. 2002. The genetics of reproductive isolation: a retrospective and prospective look with comments on ground crickets. Amer. Natur. 159: S8–S21.

JENNIONS, M. D. & M. PETRIE. 2000. Why do females mate multiply? A review of the genetic benefits. Biol. Rev. Cambridge Phil. Soc. 75:21–64.

KARLSSON, B. 1998. Nuptial gifts, resource allocation and reproductive output in a polyandrous butterfly, *Pieris napi*. Ecology 79: 2931–2940.

KATAKURA, H. 1986a. Evidence for the incapacitation of heterospecific sperm in the female genital tract in a pair of closely related ladybirds (Insecta, Coleoptera, Coccinellidae). Zool. Sci. 3:115–121.

——. 1986b. A further study of the effect of interspecific mating on the fitness of a pair of sympatric phytophagous ladybirds. Kontyû, Tokyo 54:235–242.

KATAKURA, H. & Y. SOBU. 1986. Cause of low hatchability by the interspecific mating in a pair of sympatric ladybirds (Insecta, Coleoptera, Coccinellidae): incapacitation of sperm and death of hybrid embryos. Zool. Sci. 13:315–322.

KARLSSON, B. 1995. Resource allocation and mating systems in butterflies. Evolution. 49:955–961.

KEMPENAERS, B., K. FOERSTER, S. QUESTIAN, B. C. ROBERTSON & E. L. M. VERMEIRSSEN. 2000. Distinguishing between female choice versus male sperm competition: a comment on Birkhead. Evolution 54:1050–1052.

LAMUNYON, C.W. 1994. Paternity in naturally occurring *Utetheisa ornatrix* (Lepidoptera: Arctiidae) as estimated using enzyme polymorphism. Behav. Ecol. Sociobiol. 34: 403–408.

LAMUNYON, C. W. 1999. Sperm storage by females of the polyandrons noctuid moth, *Heliothis virescens*. Animal. Behav. 59:395–402.

LAMUNYON, C. W. & S. WARD. 1999. Evolution of sperm size in nematodes: sperm competition favors larger sperm. Proc. Royal Soc. London, Series B. 266:263–267.

LAYBERRY, R. A., P. W. HALL & J. D. LAFONTANE 1998. The Butterflies of Canada.University of Toronto Press.

LEDERHOUSE, R. C. 1995. Comparative mating behavior and sexual selection in North American Swallowtail butterflies, pp.117–131. *In* Scriber, J. M., Y. Tsubaki, & R. C. Lederhouse (eds.), Swallowtail butterflies: their ecology and evolutionary biology. Scientific Publishers, Gainesville, Florida.

LEDERHOUSE, R. C. & J. M. SCRIBER. 1987. Ecological significance of a post-mating decline in egg viability in the tiger swallowtail. J. Lepid. Soc. 41: 83–93.

LEDERHOUSE R. C., M. AYRES & J. M. SCRIBER. 1989. Evaluation of spermatophore counts in studying mating systems of Lepidoptera. J. Lepid. Soc. 43:93–101.

——1990. Adult nutrition affects male virility in *Papilio glaucus*. Funct. Ecol. 4:743–751.

LEFEVRE, G. & U. B. JONSSON. 1962. Sperm transfer, storage, displacement, and utilization in *Drosophila melanogaster*. Genetica 66:195–202.

LUEBKE, H. J., J. M. SCRIBER & B. S. YANDELL. 1988. Use of multivariate discriminate analysis of male wing morphometrics to delineate the Wisconsin hybrid zone for *Papilio glaucus glaucus* and *P. g. canadensis*. Amer. Mid. Nat. 119:366–379.

MANN, T. 1984. Spermatophores. Springer-Verlag, Berlin, Germany.

MARSHALL, J. L., M. L. ARNOLD & D. J. HOWARD. 2002. Reinforcement: the road not taken. Trends Ecol. & Evol. 17:558–563

MARTIN, O. Y. & D. J. HOSKEN. 2003. The evolution of reproductive isolation through sexual conflict. Nature 423:979–982.

NEUBAUM, D. M. & M. F. WOLFNER. 1999. Wise, winsome, or weird? Mechanisms of sperm storage in female animals. Curr. Topics. Develop. Biol. 41:67–97.

NEWCOMER, S. D., J. A. ZEH & D. W. ZEH. 1999. Genetic benefits enhance the reproductive success of polyandrous females. Proc. National Acad. Sci. USA 96:10236–102241.

ONO, T.M., T. SIVA-JOTHY & A. KATO. 1989. Removal and subsequent ingestion of rival's semen during copulation in a tree cricket. Physiol. Entomol. 14: 195–202.

ORDING, G. 2001. Island Populations and trait comparisons of tiger swallowtail butterflies, *Papilio canadensis* in the Great Lakes Region. M.S. Thesis. Michigan State University, East Lansing, Michigan.

ORR, B. 1995. The evolution of the sphragis in the Papilionidae and other butterflies, pp. 155–164. *In* Swallowtail butterflies: the ecology and evolutionary biology. Scriber, J. M., Y. Tsubaki, R. C. Lederhouse (eds.), Scientific Publishers, Gainesville, Florida.

ORR, B. & M. TURELLI. 2001. The evolution of postzygotic isolation: accumulating Dobzhansky-Muller incompatibilities. Evolution. 55:1085–1094.

OTRONEN, M. 1997. Sperm numbers, their storage and usage in the fly, *Dryomyza anilis*. Proc.Royal Soc. London Series B. 264:777–782.

PAI, A. & G. YAN. 2002. Polyandry produces sexy sons at the cost of daughters in red flour beetles. Proc.Royal Soc.London. Series B, Biol. Sci. 269:361–368.

PAIR, S. D., M. L. LASTER & D. F. MARTIN. 1977. Hybrid sterility of the tobacco budworm: effects of alternate sterile and normal matings on fecundity and fertility. Ann. Entomol. Soc. Amer. 60: 952–954.

PARKER, G. A. & L. W. SIMMONS. 2000. Optimal copula duration in yellow dung flies: ejaculatory duct dimensions and size-dependent sperm displacement. Evolution 54:924–935.

PARMESAN, C., N. RYRHOLM, C. STEFANESCUS, J. K. HILL, C. D. THOMAS, H. DESCIMON, B. HUNTLEY, L. KAILA, J. KULLBERG, T. TAMMARU, W. J. TENNETT, J. A. THOMAS & M. WARREN. 1999. Poleward shifts in geographic ranges of butterfly species associated with regional warming. Nature 382:765–766.

PAVULAAN, H. & D. M. WRIGHT 2002. *Pterourus appalachiensis* (Papilionidae: Papilioninae), a new swallowtail butterfly from the Appalachian region of the United States. Taxonomic Report 3: 1–20.

PITNICK, T. & R. SNOOK. 2003. Sexual conflict and sexual selection: chasing away paradigm shifts. Evolution 57:1223–1236.

PITNICK, S. & W. D. BROWN. 2000. Criteria for demonstrating female sperm choice. Evolution 54: 1052–1056.

PITNICK, S., T. MARKOW, & G. S. SPICER. 1999. Evolution of multiple kinds of female sperm-storage organs in *Drosophila*. Evolution 53:1804–1822.

PIVNICK, K.A. & J. N. MCNEIL. 1987. Puddling in butterflies: Sodium affects reproductive success in *Thymelicus lineola*. Physiol. Entomol. 12: 461–472.

PRESGRAVES, D. C. 2002. Patterns of postzygotic isolaation in Lepidoptera. Evolution 56: 1168–1183.

PRICE, C. S. 1997. Conspecific sperm precedence in *Drosophila*. Nature 388:663–666.

PRICE, C. S., K. A. DYER & J. A. COYNE. 1999. Sperm competition between *Drosophila* males involves both displacement and incapacitation. Nature 400:449–452.

PRICE, C. S., C. H. KIM, , C. J. GRONLUND & J. A. COYNE. 2001. Cryptic reproductive isolation in the *Drosophila simulans* species complex. Evolution 55:81–922.

PRICE, C. S., C. H. KIM, J. POSLUZNY & J. A. COYNE. 2000. Mechanisms of conspecific sperm precedence in *Drosophila*. Evolution 54:2028–2037.

QVARNSTRÖM , A. 2001. Context-dependent genetic benefits from mate choice. Trends Ecol. & Evol. 16:5–7.

RAFFA, K.F., N.Y. HAVILL & E.V. NORDHEIM. 2002. How many choices can your test animal compare effectively? Evaluating a critical assumption of behavioral preference tests. Oecologia 133: 422–429.

RICE, W. R. 1996. Sexually antagonistic male adaptation triggered by experimental arrest of female evolution. Nature 381:232–234.

RIESEBERG L. 2001 Chromosomal rearrangements and speciation. Trends in Ecology & Evolution 16: 351–358.

ROBINSON, T., N. A. JOHNSON & M. J. WADE. 1994. Postcopulatory, prezygotic isolation: intraspecific and interspecific sperm precedence in *Tribolium* spp., flour beetles. Heredity 73:155–159.

SADEK, M. M. 2001. Polyandry in field-collected *Spodoptera littoralis* moths and laboratory assessment of the effects of male mating history. Ent. Exper. Appl. 98:165–172.

SAKALUK, S. K. & A. K. EGGERT. 1996. Female control of sperm transfer and intraspecific variation in sperm precedence: antecedents to the evolution of a courtship food gift. Evolution 50:694–703.

SAKALUK, S. K., J. M. SCHAUS, A-K. EGGERT, W. A. SNEDDEN & P. L. BRADY. 2002. Polyandry and fitness of offspring reared under varying nutritional stress in decorated crickets. Evolution 56:1999–2007.

SCHWARZ, D., B.J. MATTA, N.L. SHAKIR-BOTTERI, AND B.A. MCPHERON. 2005. Host shift to an invasive plant triggers rapid animal hybrid speciation. Nature 436: 546–549.

SCRIBER, J. M. 1982. Foodplants and speciation in the *Papilio glaucus* group, pp. 307–314. *In* Visser, J. H. & A. K. Minks (eds.), Proceedings of the 5th International. Symposium on Insect Plant Relationships. PUDOC, Wageningen, Netherlands.

—— 1990. Interaction of introgression from *Papilio glaucus canadensis* and diapause in producing 'spring form' Eastern tiger swallowtail butterflies, *P. glaucus*. Great Lakes Entomol. 23:127–138.

—— 1993. Absence of behavioral induction in oviposition preference of *Pailio glaucus* (Lepidoptera: Papilionidae). Great Lakes Entom. 26: 81–95.

——1994. Climatic legacies and sex chromosomes: latitudinal patterns of voltinism, diapause size and host-plant selection in 2 species of swallowtail butterflies at their hybrid zone. pp. 133–171. *In* H.V. Danks (ed.) Insect life-cycle polymorphism: theory, evolution and ecological consequences for seasonality and diapause control. Kluwer Academic Publ., Dordrecht, Netherlands.

——1996. Tiger tales: natural. history of native North American swallowtails. Amer. Ent. 42:19–32.

——2002a. The evolution of insect-plant relationships; Chemical. constraints, coadaptation and concordance of insect/plant traits. Entomologia Expt. & Appl. 104:217–235.

—— 2002b. Latitudinal and local geographic mosaics in host plant preferences as shaped by thermal units and voltinism in *Papilio* spp. (Lepidoptera). European J. Entomol. 99: 225– 239.

SCRIBER, J. M. & S. GAGE. 1995. Pollution and global climate change: plant ecotones, butterfly hybrid zones, and biodiversity, pp 319–344. *In* Scriber, J.M., Y. Tsubaki, R. C. Lederhouse, (eds.), Swallowtail butterflies: their ecology and evolutionary biology. Scientific Publishers, Inc., Gainesville, Florida.

SCRIBER, J. M., M. D. DEERING, L. FRANCKE, W. WEHLING & R. C. LEDERHOUSE. 1998a. Notes on the butterfly population dynamics of 3 *Papilio* species in south central. Florida (Highlands County). Holarctic Lepid. 5:53–62.

SCRIBER, J. M., M. D. DEERING & A. STUMP. 1998b. Evidence of long range transport of a swallowtail butterfly (*Papilio glaucus* L.) on a storm front into northern Michigan. Great Lakes Entomol. 31:151–160.

SCRIBER, J. M., R. DOWELL, , R. C. LEDERHOUSE & R. H. HAGEN. 1990. Female color and sex ratio in hybrids between *Papilio glaucus glaucus* and *P. eurymedon*, *P. rutulus* and *P. multicaudatus* (Papilionidae). J. Lepid. Soc. 44:229–244.

SCRIBER, J. M., R. C. LEDERHOUSE, & R. DOWELL. 1995. Hybridization studies with North American swallowtails, pp. 269–282. *In* Scriber, J. M., Y. Tsubaki, R. C. Lederhouse (eds.), Swallowtail butterflies: their ecology and evolutionary biology. Scientific Publishers Inc., Gainesville, Florida.

SCRIBER, J. M. AND ORDING, G. 2005 . Ecological speciation without host plant specialization: origins of a new cryptic *Papilio* species (Lepidoptera: Papilionidae)(SIP-12) Ent. Exper. Appl. 115:247–263

SCRIBER, J. M., A. STUMP, & M. DEERING. 2003. Hybrid zone ecology and tiger swallowtail trait clines in North America, pp 367–391. *In* Boggs, C., W. Watt, P. Ehrilich (eds.), Ecology and evolution taking flight: butterflies as model study systems. University of Chicago Press, Chicago, Illinois.

SCRIBER, J. M., H. ROMACK & M. D. DEERING. 2006. Not all bilateral gynandromorphs in the *Papilio glaucus* group of tiger swallowtails are interspecific hybrids: new specimens from field populations. Holarctic Lepid. *in press*.

SHAPIRO, L. H. 2000. Reproductive costs to heterospecific mating between two hybridizing katydids (Orthoptera: Tettigonidae). Ann. Ent. Soc. Amer. 93:440–446.

SILBERGLIED, R. E., J. G. SHEPERD & J. L. DICKINSON. 1984. Eunichs: the role of apyrene sperm in Lepidoptera. Amer. Nat. 123:255–265.

SIMMONS, L. W. 2001. Sperm competition and its evolutionary consequences in the insects. Princeton University Press, New Jersey. 448 pp.

SIMMONS, L. W. & R. ACHMANN. 2000. Microsatellite analysis of sperm-use patterns in the bush cricket, *Requena verticalis*. Evolution. 54:942–952.

SIMMONS, L. W. & M. SIVA-JOTHY. 1998. Sperm competition in insects: mechanisms and the potential for selection, pp.341–434. *In* Birkhead, T. R., A. P. Møller (eds.), Sperm competition and sexual selection. Academic Press. London.

SIMMONS, L. W., G. A. PARKER & P. STOCKLEY. 1999. Sperm displacement in the yellow dung fly, *Scataphaga stercoraria*: an investigation of male and female processes. Amer. Nat. 153:302–314.

SIVA-JOTHY, M. T. & R. E. HOOPER. 1996. Differential. use of stored sperm during oviposition in the damselfly, *Calopteryx splendens xanthostoma* (Charpentier). Behav. Ecol. Sociobiol. 39:389–393.

SMEDLEY, S.R. & T. EISNER. 1996. Sodium: a male moth's gift to its offspring. Proc. Nat. Acad. Sci. (USA) 93: 809–813.

SMITH, R. L. 1984. Sperm competition and the evolution of animal mating systems. Academic Press, San Diego, California, 687pp.

SPERLING, F. A. H. 1990. Natural hybrids of *Papilio* (Insecta: Lepidoptera): poor taxonomy or interesting evolutionary problem? Can. J. Zool. 68:1790–1799.

——1993. Mitochondrial DNA variation and Haldane's rule in the *Papilio glaucus* and *P. troilus* species groups. Heredity 71: 227–233.

——2003. Butterfly molecular systematics: from species definitions to higher level phylogenies. Pp 431–458 *In*: Boggs, CL, Watt WB, & Ehrlich PR (eds) Butterflies:Ecology and Evolution taking flight. Univ. Chicago Press.

STJERNHOLM, F. & B. KARLSSON. 2000. Nuptial gifts and the use of body reserves for reproduction in the green-veined white butterfly, *Pieris napi*. Proc. Roy. Soc. London. B 267: 807–811.

STOCKLEY, P. 1997. Sexual conflict resulting from adaptations to sperm competition. Trends Ecol. & Evol. 12:154–159.

STUMP, A. D. 2000. Lack of cryptic reproductive isolation between *Papilio canadensis* and *Papilio glaucus* and population genetics near their hybrid zone. M.S. Thesis. Michigan State University, East Lansing, Michigan.

SUGAWARA, T. 1979. Stretch reception in the bursa copulatrix of the butterfly, *Pieris rapae crucivora*, and its role in behavior. J. Comp. Physiol. A 130:191–199.

THORNHILL, R. & J. ALCOCK. 1983. The evolution of insect mating systems. Harvard University Press, Cambridge, Massachusetts, pp 547.

TREGENZA, T. 2003. The battle between the sexes. Nature. 423:929–930.

TREGENZA, T. & N. WEDELL. 2002. Polyandrous females avoid costs of inbreeding. Nature. 415:71–73.

TREGENZA, T. N. WEDELL, D. J. HOSKEN & P. I. WARD. 2003. Maternal eeffects on offspring depend on female mating pattern and offspring environment in yellow dung flies. Evolution 57: 297–304.

TSCHUDI-REIN, K. & G. BENZ. 1990. Mechanisms of sperm transfer in female *Pieris brassicae* (Lepidoptera: Pieridae). Ann. Entomol. Soc. Amer. 83:1158–1164.

TURELLI, M., N. H. BARTON & J. A. COYNE. 2001. Theory and Speciation. Trends Ecol. & Evol. 16: 330–343.

VAHED, K. 1998. The function of nuptial. feeding in insects: review of empirical studies. Biological. Rev. Cambridge Phil. Soc. 73: 43–78.

VIA, S. 2002. The ecological genetics of speciation. American Naturalist 109: S1–S7

WAAGE, J. K. 1979. Dual function of the damselfly penis: sperm removal and transfer. Science 203:916–918.

WADE, J. M., H. PATTERSON, N. CHANG & N. A. JOHNSON. 1993. Post-copulatory, prezygotic isolation in flour beetles. Heredity 71:163–167.

WARD, P. I. 1993. Females influence sperm storage and use in the yellow dung fly *Scathophaga stercoraria* (L). Behav. Ecol. Sociobiol. 32:313–319.

——. 1998. A possible explanation for cryptic female choice in the yellow dung fly, *Scatophaga stercoraria* (L.). Ethology 104, 97–110.

——. 2000. Cryptic female choice in the yellow dung fly, *Scatophaga stercoraria* (L.). Evolution 54:1680–1686.

WATANABE, M. 1988. Multiple matings increase the fecundity of the yellow swallowtail butterfly, *Papilio xuthus* L., in summer generations. J. Insect Behav. 1:17–29.

WATANABE, M. & M. HIROTA. 1999. Effects of sucrose intake on spermatophore mass produced by male swallowtail butterfly *Papilio xuthus* L. Zool. Sci. 3:509–516.

WATANABE, M. & K. SATO. 1993. A spermatophore structured in the bursa copulatrix of the small white *Pieris rapae* (Lepidoptera: Pieridae) during copulation and its sugar content. J. Res. Lepid. 32:26–36.

WATANABE, M., M. BON'NO & A. HACHISUKA. 2000. Eupyrene sperm migrates to spermatheca after apyrene sperm in the swallowtail butterfly, *Papilio xuthus* L. (Lepidoptera: Papilionidae). J. Ethology 18:91–99.

WEDELL, N. & P. COOK. 1998. Determinants of paternity in a butterfly. Proc. Royal. Soc. London, Series B. 265:625–630.

WEDELL, N, M., .J. G. GAGE & G. A. PARKER. 2002. Sperm competition, male prudencce and sperm-limited females. Trends Ecol. Evol. 17: 313–320.

WIKLUND, C. 2003. Sexual selection and the evolution of butterfly mating systems, pp 67–90. *In* Boggs, C., W. Watt, & P. Ehrlich (eds.), Ecology and evolution taking flight: butterflies as model study systems. University of Chicago Press, Chicago, Illinois.

WIKLUND, C., A. KAITALA, V. LINDFORS & J. ALBENIUS. 1993. Polyandry and its efffect on female reproduction in the green-veined white butterfly (Pieris napi L.). Behav. Ecol. & Sociobiol. 33: 25–33.

WILSON, N., S. C. TUBMAN, P. E. EADY & G. W. ROBERSTON. 1997. Female genotype affects male success in sperm competition. Proc. Royal. Soc. London, Series B. 264:1491–1495.

WOODS, H. A., C. E. SORENSEN, A. STEPHENSON & J. F. HARRISON. 2001. A simple allozyme method for distinguishing all life stages of *Manduca sexta* and *M. quinquemaculata*. Entomol. Expt. Appl. 98:109–113.

YASUI, Y. 1998. The 'genetic benefits' of female multiple mating reconsidered. Trends Ecol. & Evol. 13: 246–250.

ZEH, J.H. & D. W. ZEH. 1994. Last-male sperm precedence breaks down when females mate with three males. Proc. Roy. Soc. Lond. Ser. B 257: 287–292.

ZEH, J. A. & ZEH, D. W. 2001. Reproductive mode and genetic benefits of polyandry. Animal Behav. 61:1051–1063.

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CAVIHEMIPTILOCERA, A NEW GENUS FOR *MYELOIS EXOLETA* ZELLER (LEPIDOPTERA: PYRALIDAE: PHYCITINAE)

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ABSTRACT. A new genus, *Cavihemiptilocera* Neunzig, is proposed for *Myelois exoleta* Zeller, a species occurring in South America. The new genus is described and illustrations are provided for the previously unknown male as well as for the female.

Additional key words: Phycitinae, Brazil, Colombia, Ecuador.

Zeller in 1881 described *Myelois exoleta* along with other new species of Phycitinae collected in Colombia, South America. Ragonot (1893) moved the species from the broadly conceived category *Myelois* to his more narrowly defined new genus *Hemiptilocera*. Heinrich (1956) in his revision of the American phycitines reluctantly followed Ragonot in including *exoleta* in *Hemiptilocera*. He pointed out that the placement was tenuous because the species was known only from the female type specimen, and that his examination of the genitalia of the type revealed features not found in the genitalia of other species included in *Hemiptilocera*.

I have examined recently collected South American phycitines in the National Museum of Natural History, Washington, D.C., U.S.A. and the Becker Collection, Brasilia, Brazil, and have found additional specimens of *exoleta*, both males and females. A study of the males does not support keeping the species in *Hemiptilocera*. Particularly pertinent are differences in the antenna, the gnathos, the sacculus, and the aedoeagus. Therefore, I propose in this paper a new genus for *exoleta* .

Abbreviations used for depositories of types and other specimens are as follows: Becker Collection, Universidade de Brasilia, Brazil [VOB]; National Musuem of Natural History, Washington, D.C., U.S.A. [USNM]; Natural History Museum, London, England [BMNH]; North Carolina State University Insect Collection, Raleigh, North Carolina, U.S.A. [NCSU].

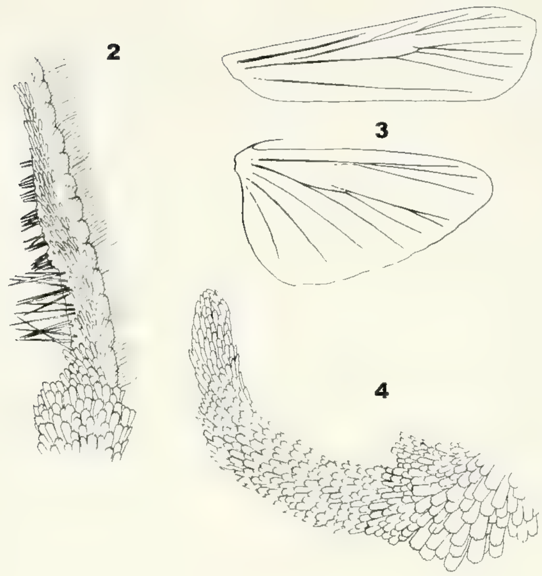
Cavihemiptilocera Neunzig, New genus

Type species. - *Myelois exoleta* Zeller 1881

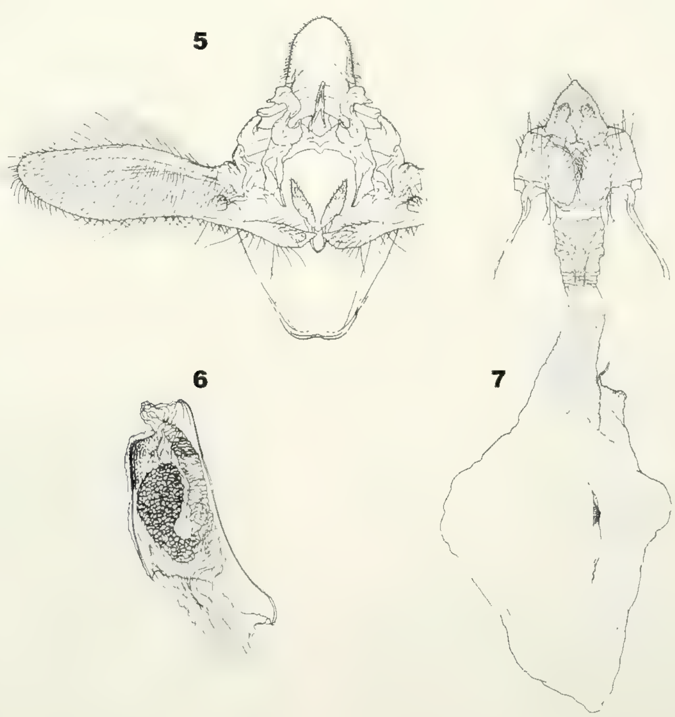
Diagnosis. The base of the shaft of the antenna has a row of long, slender spines followed closely distally by clusters of short, slender spines (Fig. 2), the transtilla bears posteriorly strongly developed, sinuous hooks (Fig. 5), and the dorsum of each papilla analis has a shallow, sclerotized pocket (Fig. 7).

Description. Antenna of male (Fig. 2): shaft with shallow sinus basally and associated row of long slender, straight spines (spines about 1 1/2 times as long as diameter of base of shaft); shaft just distad of sinus with additional row of about six clusters of short, straight spines (spines about 1/2 length of spines in sinus); sensilla trichodea (cilia) about 3/4 as long as diameter of base of shaft. Antenna of female: simple. Frons of both sexes: convex, smooth-scaled to slightly rough-scaled. Vertex of both sexes: rough-scaled. Labial palpus of both sexes (Fig. 4): upcurved, reaching vertex. Maxillary palpus of both sexes: simple, short-scaled. Haustellun: well developed in both sexes. Ocellus: present in both sexes. Forewing of male (Fig 3): smooth-scaled, with 11 veins; R_{3+4} and R_5 stalked for about 3/5 distance beyond cell; M_1 from near anterodistal angle of cell; M_2 and M_3 shortly fused at base; CuA_1 from near posterodistal angle of cell; CuA_2 from well before posterodistal angle of cell. Hindwing of male (Fig. 3): with 8 veins (1A, 2A, and 3A together treated as one vein); $Sc+R_1$ and Rs contiguous, or close together, for about 1/2 distance beyond cell; M_2 and M_3 fused for about 2/3 distance beyond cell; CuA_1 from near posterodistal angle of cell; CuA_2 from well before posterodistal angle of cell. Female wings as in male. Male abdominal segment 8 with ventral tuft of scales; scales forming tuft numerous, thin, setalike, slightly curved. Female abdominal segment 8 simple. Male genitalia (Figs. 5, 6): uncus hoodlike; gnathos with distal element a short hook; transtilla strongly developed, distally with pair of large, sinuate, partly-serrate, broad hooks; juxta V-shaped, with posterolateral lobes pointed and with short setae; valva well developed, moderately slender with strongly developed, knoblike lobe arising from basal surface; sacculus well integrated into rest of valva; aedoeagus short, robust, in part spinose distally; vesica with large, globular, dense cluster of short cornuti; vinculum shorter than greatest width. Female genitalia (Fig. 7): papilla analis each with shallow, sclerotized dorsal pocket; collar of abdominal segment 8 with median-dorsal, invaginated, sclerotized, V-shaped recess and associated pair of subventral, elongate, sclerotized and scobinate lobes; ostium bursae heavily sclerotized, ventrally with V-shaped, groved structure; ductus bursae about 1/2 as long as corpus bursae, strongly scobinate throughout its length; corpus bursae heartshaped, with posterior half

FIG. 1. Habitus of male *Cavihemiptilocera exoleta*.



FIGS. 2–4. Antenna, wings and labial palpus of male *Cavihemiptilocera exoleta*. 2, left antenna, frontal view. 3, right forewing and hindwing venation, dorsal view. 4, left labial palpus, lateral view.



FIGS. 5–7. Genitalia of *Cavihemiptilocera exoleta*. 5, male, ventral view, right valva and aedoeagus omitted. 6, aedoeagus. 7, female, ventral view (dorsal pocket of each papilla analis showing through ventral integument)

scobinate; signum a small, invaginated, dense concentric cluster of scobinations; ductus seminalis arising from corpus bursae near junction of ductus bursae and corpus bursae.

Etymology. The genus name is a combination of the Latin *cav* - (hollow or cave) referring to the unique dorsal pockets on the papillae anales, and the related genus *Hemiptilocera*. The gender of *Cavihemiptilocera* is feminine.

Cavihemiptilocera exoleta (Zeller), new combination (Figs. 1–7)

Myelois exoleta Zeller 1881: 201.
Hemiptilocera exoleta (Zeller). Ragonot 1893: 146.
Type locality. Honda, Colombia

Description. Head: frons and vertex ochre to dark brown; labial palpus outwardly mostly dark brown, basal segment ochre in some specimens; maxillary palpus mostly dark brown with ochre or reddish brown scales in some specimens. Thorax: dorsum mostly ochre or pale brown washed with dark brown. Forewing: length 11.0–12.5 mm; ground color brown; patch of reddish brown and black at base; small ochre patch subbasally near costa; antemedial line obscure, ochre, distinguishable at costa where it is bordered proximally and distally with black; postmedial line weak to moderately distinct, ochre, bordered proximally by black band; terminal area washed with reddish brown and ochre and with black, longitudinal streaks on anterior half and row of black transverse, terminal spots; discal spots replaced by large distinctive, reddish brown and black lunule. Hindwing: mostly hyaline, black along margins of wing in male; mostly brown, black along margins of wing in female. Male and female genitalia as described for genus.

Material Examined. Brazil: 1 ♀, Amazonas, Manaus, BR-174 km. 64, 2f–3 km. 7 Faz. Porto Alegre, 2°22'20" S/59°56'29" W, R-3304, 13-14/81 1996, R.W. Hutchings Col., 15W UV light trap at 1,200-c., genitalia slide 6147 HHN [USNM]. Colombia: 1 ♀ (type), (Cundinamarca), Honda, (Petersen) [BMNH]. Equador: 2 ♂, Napo, Misahualli, 450 m, XII 11 1992, V.O. Becker, genitalia slide 5848 HHN [VOB] [NCSU].

Remarks. A comparison of *Cavihemiptilocera* and *Hemiptilocera chinographella* Ragonot (type species of *Hemiptilocera*) shows: the male genitalia of *Cavihemiptilocera* have the gnathos entire distally, the sacculus well integrated into the rest of the valva, and the vesica has a large, globular, dense cluster of short cornuti; whereas, the male genitalia of *Hemiptilocera* have gnathos notched distally, the sacculus partially separated from the rest of the valva, and the vesica has a single cornutus.

The female genitalia of *Cavihemiptilocera* have: each papilla analis with a sclerotized dorsal pocket, the eighth abdominal collar and a V-shaped recess, in contrast to the female genitalia of *Hemiptilocera* that are without sclerotized dorsal pockets in each papilla analis and the eighth abdominal segment is without a V-shaped recess.

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LITERATURE CITED

HEINRICH, C. 1956. American moths of the subfamily Phycitinae. United States National Museum Bulletin 207: 1–581.

RAGONOT, E. -L. 1893. Monographie des Phycitinae et des Gallerinae. *In* Romanoff, N.M. Mémoires sur les Lépidoptères, 7, Imprimerie Générale Lahure, Paris. 1–658.

ZELLER, P. C. 1881. Columbische, Chilonden, Crambiden und Phycideen. Horae Societatis Entomologicae Rossicae 16: 154–256.

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SOME DISTASTEFUL ASIAN PAPILIONINAE (PAPILIONIDAE)

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ABSTRACT. Western Himalayan populations of three Asiatic *Papilio* L. species appear to be distasteful in varying degrees to birds. These include the polymorphic *Papilio polytes* L. which was considered a classic Batesian mimic of distasteful *Pachliopta* Reakirt. The Indian population of *polytes*, with three female forms, is a case of sympatric polymorphism in a distasteful species with warning coloration.

Additional key words: Müllerian mimicry; *Papilio*; polymorphic model

INTRODUCTION

Batesian mimicry, referring to a system comprising palatable species and unpalatable models, and Müllerian mimicry, involving similar-looking, unpalatable species, are well known examples of adaptive evolution by natural selection. Of the over 200 species of *Papilio* L. known, at least one W. African species (*antimachus* Drury) is known to be chemically protected in the adult stage (Watson & Whalley 1983). Several species are believed to be Batesian mimics of chemically defended moths and butterflies (Clarke & Sheppard 1960, 1962 ; Brower & Brower 1962 ; Clarke et al. 1968 ; Watson & Whalley 1983; etc.). Although the larvae of all *Papilio* butterflies are believed to be chemically protected by unpleasant taste and smell (Wynter-Blyth 1957; Klots & Klots 1959), this was not believed to be carried over to the adult stage except in the case of *antimachus*.

MATERIALS & METHODS

In a pilot study undertaken at Jones Estate, Bhimtal, in Nainital district, Uttaranchal, India (elevation 1500 m; latitude 29°20'41" N and longitude 79°36'15" E) in the outermost range of the Kumaon Himalaya, I presented >560 freshly collected, wild butterflies belonging to 86 species to wild, free ranging, foraging parties of birds in > 256 encounters over a period of 4 years (1999–2002). One or more of three *Papilio* species, i.e. *polyctor* Boisduval, *protenor* Cramer and *polytes* L. formed part of the presentation on 109 occasions. A total of 10 *polyctor* (9♂, 1♀), 9 *protenor* (8♂ , 1♀) and 18 *polytes* (12♂, 6 ♀) were presented. Each specimen, if not devoured, was presented several times, sometimes on the same day, until it was too dry to be attractive to the birds.

The birds consisted of one family of White Crested Laughing Thrushes (*Garrulax leucolophus*), whose composition varied from 2 to 7 birds during the period of observation and White Throated Laughing Thrushes (*Garrulax albogularis*) in groups varying from 4 to >60 seasonally. Casual foraging species included Blue Whistling Thrushes (*Myiophonus caeruleus*) and a Yellowcheeked Tit (*Parus xanthogenys*).

Laughing Thrushes are not known to attack butterflies on the wing. They feed on insects, berries and other vegetable matter (Ali 1962). White Crested and White Throated Laughing Thrushes spend most of their foraging time turning over dead leaves on the ground and investigating the bark and foliage of trees (Whistler 1935; Ali 1949).

They are very fond of live moths (*pers. obs.*). Initially the birds in this study were wary of dead butterflies but they soon developed a taste for them, especially control species belonging to Nymphalinae, of which 100% were eaten.

The lack of experience on the part of the birds and their evident willingness to learn proved advantageous, since they examined and tried to eat (at least once) every species presented, including known unpalatable species belonging to *Delias* Hübner, *Danaus* Latreille and *Pachliopta* Reakirt. White Crested Laughing Thrushes displayed a high degree of prey recognition at the species level. Many White Throated Laughing Thrushes ignored the butterflies completely throughout the study. The birds were observed from a distance of 3–4 m, initially through a wire mesh screen and later in the open.

RESULTS

Entire butterflies were offered, except on three different occasions when, after repeated rejections, the wing scales of 1 *polyctor* and 2 *protenor* specimens were wiped off and the wing shape altered to circumvent possible preconditioned visual aversion on the part of the birds. The *polyctor* was eaten but both the *protenor* continued to be ignored.

One ♂ 1 ♀ *polyctor*, 1 ♂ *protenor* and 4 ♂ 2 ♀ *polytes* were entirely eaten. The *protenor* was the only butterfly eaten by a Yellow-cheeked Tit on its single visit to the site. Ten percent of *polyctor*, 0% of *protenor* and 11.1% of *polytes* were partially eaten, usually the head and either thorax or abdomen. In all, 30% of *polyctor*,

11.1% of *protenor* and 44.4 % of *polytes* were entirely eaten, compared with 77% to 100% (mean 95%) for control species (*Colias fieldii* Ménetriés 77%; *Graphium sarpedon* Felder 90%; *Vanessa indica* Herbst 100%; *Kaniska canace* Linné 100%; *Symbrenthia lilaea* Hewitson 100% ; *Precis iphita* Cramer 100% ; *Junonia lemonias* Linné 100 % ; *Lethe rohria* Fabricius 90%; *Melanitis leda* Linné 100 % ; *Deudoryx epijarbas* Moore 95%) presented along with the *Papilio* species.

On one occasion, a White Crested Laughing Thrush that ate the abdomen and hindwings of a ♂ *polytes* and nothing else exhibited signs of distress immediately afterwards, opening its beak repeatedly as if to call but not emitting any sound. Such behavior was never observed in connection with the controls.

DISCUSSION

P. polyctor is not known to be mimetic, while *protenor* females have been proposed as Batesian mimics of the *Atrophaneura varuna* White group (Batwings) and three of the four female forms of the polymorphic *polytes* are considered classic Batesian mimics of *Pachliopta* (Evans 1932; Wynter-Blyth 1957; Clarke & Sheppard 1972; Larsen 1987). Peile (1937), quoting from T.R.D. Bell's series "Common Butterflies of the Plains of India" published in the *Journal of the Bombay Natural History Society*, stated that "the (*Pachliopta*) group is protected by very unpleasant smell and taste. Birds will not eat them nor will lizards willingly or readily. *P. polytes*, of a different group, is without these qualities ...". However, he did not qualify this statement further.

The male of *polytes* and one female form, *cyrus*, which occurs throughout the insect's range, are non-mimetic. The second female form, *romulus*, resembles *Pachliopta hector* L. and both are restricted to India and Sri Lanka. The nomino-typical form primarily resembles *Pachliopta aristolochiae* Fabricius and the two exhibit similar variation in wing pattern throughout their range from the Himalayas to Sri Lanka, Japan and Sulawesi. In addition, the typical from also resembles *Pachliopta polyphontes* Boisduval and *Pachliopta polydorus* L. in part of S.E. Asia. The form *theseus* of *polytes* resembles the black form of *aristolochiae* and both occur in parts of the Philippines and parts of Indonesia, while *Pachliopta atropos* Staudinger is a possible additional co-model on Palawan (Clarke & Sheppard 1972). In the present study, although three female forms of *polytes* occur in the area, only the *cyrus* form and males were used to preclude possible preconditioned visual aversion to the mimetic forms on the part of the birds. The possibility of significant differences in palatability between the female forms is unlikely, since all the forms in a given area (three in India and Sri Lanka) are obtainable from a single batch of eggs (Fryer 1913; Clarke & Sheppard 1972).

The above data strongly suggest that these three *Papilio* species are distasteful and that *polytes* is a Müllerian co-model rather a Batesian mimic of *Pachliopta*, at least in parts of its range. *P. polyctor* and *polytes* appear to be moderately distasteful while *protenor* is quite distasteful to birds at the study site (Table 1).

In the larval stage, these three species feed on members of the citrus family (Rutaceae). *P. polyctor* and *protenor* feed on *Xanthoxylum armatum* DC, while *polytes* feeds on a variety of rutaceous plants and has been bred on *Murraya königii* Spreng. and cultivated *Citrus* L. in the study area. Troidine swallowtails are known to sequester aristolochic acids from their

TABLE 1. Pooled responses of White Crested and White Throated Laughing Thrushes to freshly collected, wild, dead butterflies. Butterflies that were manipulated for +5 seconds by one or more birds and then rejected are recorded in column 6. The response score (column 7) was calculated from scores recorded for individual presentations: 0 = ignored, flung aside, pecked briefly or repeatedly but not eaten (this information was recorded in words); 1= the butterfly was partially eaten, usually the head and either thorax or abdomen (specimens preserved in my collection) and 2 = the entire body, but not necessarily the wings, was eaten. Specimens were collected at the study site in Jones Estate and at Ranibagh (altitude 600 m), 20 km. south by road from Jones Estate, mainly in March–April and October–November.

1 Species	2 Specimens Presented	3 # of encounters	4 # entirely eaten		5 # partially eaten		6 # of times rejected		7 Response Score		
			Specimens	%	Specimens	%	Specimens	% of encounters	Max possible	Actual	%
Control	123	133	117	95.1	3	2.4	3	2.2	246	238	95.9
polyctor	10	33	2	20	2	20	4	12	20	6	30
protenor	9	32	1	11	0	0	4	12.5	18	2	11.1
polytes	18	49	6	33	4	22	7	14	36	16	44.4

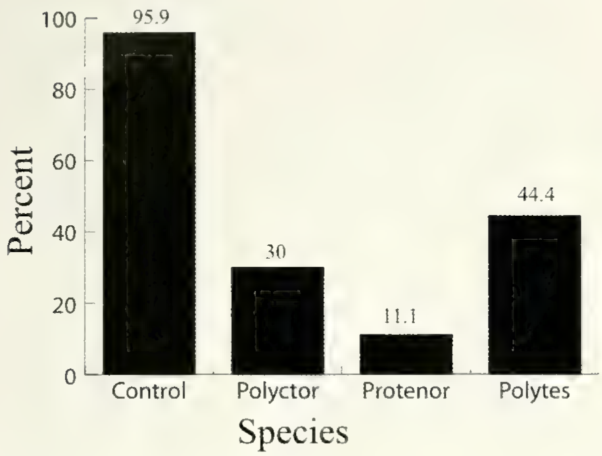

FIGURE 1. Palatability index for the percentage of butterflies entirely or partially eaten by wild birds, based on response score described in Table 1. Butterflies were presented randomly.

hostplants (Brown *et al.* 1991) and it is possible that some *Papilio* butterflies, such as the species considered in this paper, have retained the ability to sequester aromatic or distasteful compounds from their larval hostplants. Although some *Papilio* species are known to be palatable to birds, such as the N. American *glaucus* L. and *palamades* Drury, which have been used as controls (95% eaten) in another study (Ritland & Brower 1991), both species do not feed on Rutaceae but on Rosaceae, Oleaceae, Salicaceae, Betulaceae, Lauraceae and Magnoliaceae (Scriber *et al.* 1975 ; Watson & Whalley 1983; Daccordi *et al* . 1988). In the present study, *Graphium* Scopoli species that feed on Lauraceae were found to be attractively palatable to the birds (unpublished) and one was used as a control.

In this study, the spring and summer broods of *polyctor*, the spring brood of *protenor* and spring and autumn broods of *polytes* were used. The results do not suggest any noticeable difference in distastfulness between the broods.

The present study was carried out using wild, free-ranging birds which are not habitual predators on butterflies but generalized insectivores. The study involved the random presentation of wild butterflies. The birds could be observed only while they were at the study site. Since they usually departed soon after eating, possible distress behavior or even regurgitation could not always be observed. Rigorous measurements of manipulation time, number of times pecked and other minutiae were not always possible in the melée caused by a large number of birds feeding on a small patch of ground. The birds at times arrived and devoured everything in sight and at other times ignored everything, including controls, having evidently found sufficient food elsewhere.

Although extrapolation of the results obtained from the small number of *Papilio* specimens offered in this study must be done with caution, there is little doubt that at least some populations of the three *Papilio* species are distasteful in varying degrees to some birds.

The present findings prompt a re-interpretation of the relationship between *polytes* and *Pachliopta* . The classic Batesian interpretation of *polytes-Pachliopta* mimicry predicted that only *polytes* benefits at the expense of *Pachliopta*, which it "parasitises", and predators, which it deceives into shunning palatable prey. The new Müllerian interpretation suggests that the shared aposematic signals of the co-models (*polytes* and *Pachliopta* spp.) result in enhanced predator learning and the benefits of this accrue to all the butterfly species involved. The relationship between the butterflies is one of asymmetrical Müllerian mimicry, since *polytes* appears to be only moderately distasteful while the *Pachliopta* genus is certainly more distasteful, with aristolochic acids in the body tissue.

The distastefulness of *polytes* also explains the persistence of the non-mimetic female form *cyrus* over the entire range of the species. Although *cyrus* comprises only 5% of the total female population in parts of southern India where *aristolochiae*, *hector* and the corresponding female forms of *polytes* are very common (Larsen 1987), it predominates in the western Himalayan foothills where *hector* is absent and *aristolochiae* scarce or absent (Peile 1937; Wynter-Blyth 1957) but where *polytes* is as common as in other parts of its range. Indeed, the presence or absence of its co-models hardly affects the abundance of *polytes* over its range, as in the Himalayan foothills of Himachal Pradesh, India, where it is not uncommon despite the fact that none of its co-models occur (DeRhe-Philippe 1931).

Polymorphism in distasteful species with warning coloration is an unusual phenomenon (Joron & Mallet 1998 ; Kapan 2001), since genetic analysis of Müllerian mimicry indicated that selection is for monomorphism rather than polymorphism (Turner & Crane 1962; Sheppard 1963; Emsley 1964). In other known polymorphic Müllerian co-models, such as *Heliconius cydno* Doubleday & Hewitson and *Heliconius erato* L., different forms of the same species are rarely sympatric (Joron & Mallet 1998). In the very likely event that all populations of *polytes* are as distasteful as the western Himalayan one, the case of *polytes* in southern India is unusual, since the two mimetic forms of the female which occur there are roughly equally abundant (Peile 1937), eg. *hector*-like form 50.4% and *aristolochiae*-like form 45.7% at a single location (Larsen 1987).

It has been proposed (Kapan 2001) that geographical

variation in selection for mimicry coupled with weak selection against forms when they are common explains the existence of polymorphic Müllerian co-models. Although this proposition is applicable to certain cases, notably *Heliconius* Kluk, it cannot be applied to the case of sympatric polymorphism in *polytes* in southern India.

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LITERATURE CITED

ACKERY, P.R. & R.I. VANE-WRIGHT. 1984. Milkweed butterflies—their cladistics and biology. Brit. Mus. (N.H.). London. 425 pp.

ALI, S. 1949. Indian Hill Birds. Oxford Univ. Press, Delhi. 42+426 pp.

——. 1962. The Birds of Sikkim. Oxford Univ. Press, Delhi. 30+414 pp; 26 pl.

BROWER, L.P. & J. VAN Z. BROWER. 1962. The relative abundance of model and mimic butterflies in natural populations of the *Battus philenor* mimicry complex. Ecology 43: 154–158.

BROWN, K.S. JR., J.R. TRIGO, R.B. FRANCINI, A.B. BARROS DE MORAIS & P.C. MOTTA. 1991. *In* Plant-Animal Interactions (eds. Price, P.W., T.M. Lewinsohn, G.W. Fernandes & W.W. Benson). Wiley, New York. 375–402 pp. quoted by Vane-Wright, R.I. 1991. A case of self-deception. Nature, London. 350: 460–461.

CLARKE, C.A. & P.M. SHEPPARD. 1960. The evolution of mimicry in the butterfly *Papilio dardanus*. Heredity 14: 163–173.

——. 1962. The genetics of the mimetic butterfly *Papilio glaucus*. Ecology 43: 159–161.

CLARKE, C.A. & P.M. SHEPPARD & I.W.B. THORNTON. 1968. The genetics of the mimetic butterfly *Papilio memnon* L.. Phil. Trans. R. Soc. Lond. B 254: 37–89.

CLARKE, C.A. & P.M. SHEPPARD. 1972. The genetics of the mimetic butterfly *Papilio polytes* L.. Phil. Trans. R. Soc. Lond. B 263: 431–458.

DACCORDI, M., P. TRIBERTI & A. ZANETTI. 1988. The Macdonald Encyclopedia of Butterflies and Moths. Macdonald, London. pp. 383.

DERHÉ-PHILIPPE, G.W.V. 1931. The butterflies of the Simla Hills. J. Bomb. Nat. Hist. Soc. 35: 172–183.

EMSLEY, M. G. 1964. The geographical distribution of the color-pattern components of *Heliconius erato* and *Heliconius melpomene* with genetical evidence for the systematic relationship between the two species. Zoologica 49: 245–286.

EVANS, W.H. 1932. The Identification of Indian Butterflies. 2nd ed.. Bombay Nat. Hist. Soc. 10+454 pp.

FRYER, J.C.F. 1913. An investigation by pedigree breeding into the polymorphism of *Papilio polytes*, Linn.. Phil. Trans. R. Soc. Lond. B. 204: 227–254.

JORON, M. & J.L. MALLET. 1998. Diversity in mimicry: paradox or paradigm. Trends Ecol. Evol. 13 : 461–466.

KAPAN, D.D. 2001. Three butterfly system provides a field test of Müllerian mimicry. Nature, London, 409: 338–340.

KLOTS, A.B. & E.B. KLOTS. 1959. Living Insects of the World. Hamish Hamilton, London. 304 pp.

LARSEN, T.B. 1987. The butterflies of the Nilgiri mountains of Southern India. J. Bombay Nat. Hist. Soc. 84: 26–54.

PEILE, H. D. 1937. A Guide to Collecting Butterflies of India. Staples, London. 14+312 pp.

RITLAND, D.B. & L.P. BROWER. 1991. The viceroy butterfly is not a Batesian mimic. Nature, London 350: 497–498.

SCRIBER, J.M., R.C. LEDERHOUSE & L. CONTARDO. 1975. Spicebush, *Lindera benzoin*, a little known food plant of *Papilio glaucus* (Papilionidae). J. Lep. Soc. 29: 10–14.

SHEPPARD, P.M. 1963. Some genetic studies of Mullerian mimics in butterflies of the genus Heliconius. Zoologica 48 : 145–154.

TURNER, J.R.G. & J. CRANE. 1962. The genetics of some polymorphic forms of the butterflies Heliconius melpomene Linnaeus and Heliconius erato Linnaeus. 1. Major genes. Zoologica 47 : 141–152.

WATSON, A., P.E.S. WHALLEY & W.D. DUCKWORTH. 1983. The Dictionary of Butterflies and Moths in Color. Peerage, London. 14+296 pp.

WHISTLER, H. 1935. Popular Handbook of Indian Birds. Gurney & Jackson, London. pp 28–30 .

WINTER-BLYTH, M.A. 1957. Butterflies of the Indian Region. Bombay Natural History Society, Bombay. 20+523 pp.

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STABILIZING THE NOMENCLATURE OF FABRICIAN NAMES OF NORTH AMERICAN HAIRSTREAKS (LYCAENIDAE: THECLINAE: EUMAEINI)

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ABSTRACT. Four actions are taken to preserve nomenclatural stability of Nearctic hairstreak names proposed by Fabricius. Following the provisions of ICZN Article 23.9.1, *Thecla liparops* Le Conte, 1833 is made a ***nomen protectum*** and *Hesperia anacreon* Fabricius, 1793 is made a ***nomen oblitum***. *Thecla m-album* Boisduval & Le Conte, 1833 is made a ***nomen protectum*** and *Hesperia euripides* Fabricius, 1793 is made a ***nomen oblitum***. *Lycus niphon* Hübner, [1819] is made a ***nomen protectum*** and *Hesperia plautus* Fabricius, 1793 is made a ***nomen oblitum***. The name *Hesperia cecrops* Fabricius, 1793 cannot be determined definitively from the original description and might apply to different biological species. We designate a ***neotype*** for *Hesperia cecrops* Fabricius, 1793 following the provisions of ICZN Article 75.3, with the new type locality of Savannah, Georgia, USA. New information on the identity of *Papilio mars* Fabricius, 1776 and *Hesperia titus* Fabricius, 1793 is consistent with current usage. The identity of *Hesperia columella* Fabricius, 1793 was corrected previously, and *Papilio ixion* Fabricius, 1775 remains a *nomen dubium*.

Additional key words: ICZN Article 23.9.1, Fabricius, Icones, Jones, Nearctic, Taxonomic Stability.

Between 1775 and 1807, Johann Christian Fabricius named 1,648 lepidopteran species (Zimsen 1964), including about 35 that belong to—or have been thought to belong to—the Eumaeini (Lycaenidae: Theclinae) (Robbins & Lamas in prep.). The exact number is unclear because the identity of many Fabrician lycaenid species has been uncertain (e.g., Druce 1907: 568, Draudt 1919–1920: 825). Few types are extant (Zimsen 1964). Verbal descriptions were rarely sufficiently detailed to identify species. Descriptions were not accompanied by published illustrations, and some names that were illustrated later in unpublished manuscripts were not necessarily the same species that Fabricius had originally described (Robbins & Lamas in prep.). Finally, type localities were usually inaccurate.

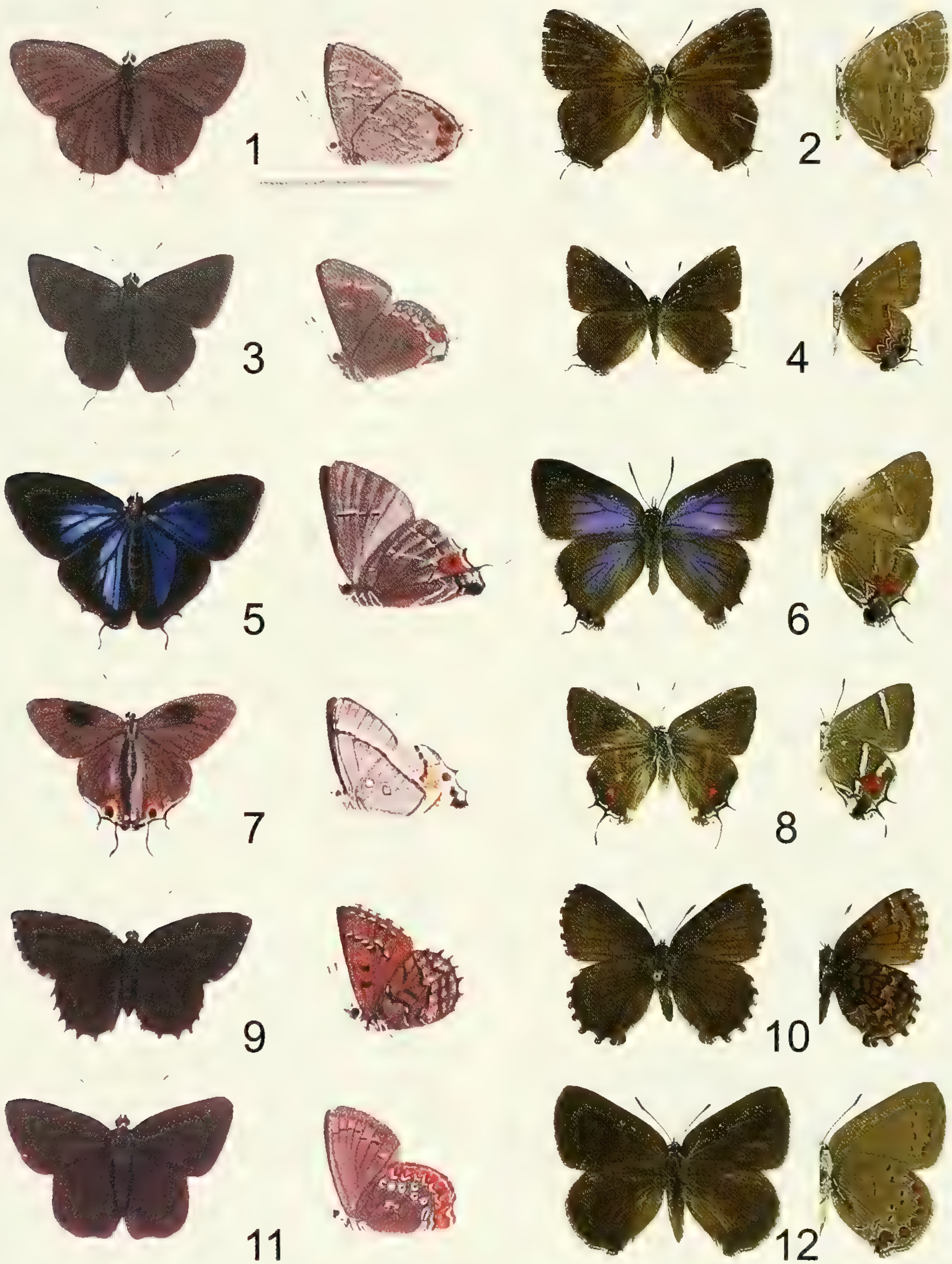
In one of his later works Fabricius (1793) sometimes referenced illustrations in an unpublished book by William Jones [?–1818] called the "Icones" (Lamas 1979 and included references). This book was never published, and the manuscript now belongs to the Hope Department of Entomology, University of Oxford, England (Smith 1986). Illustrations from the manuscript were used to identify some Neotropical Eumaeini (Robbins 2004), but the application of Fabrician names that belong to the Nearctic Eumaeini has not been reviewed. As detailed in this paper, the stability of four North American names that have been used widely and consistently for more than a century is jeopardy. The primary purpose of this paper is to review and stabilize the nomenclature for those Fabrician names that refer to the Nearctic Eumaeini. The name of one species that occurs in southern Texas (*Hesperia herodotus* Fabricius) will be treated elsewhere (Robbins & Lamas in prep.) because it is primarily a Neotropical species (Robbins & Duarte 2005).

MATERIALS AND METHODS

Fabrician names that belong to the Nearctic Eumaeini were determined by a search of the literature and by examining a set of photographic color slides of Jones' Icones made by the Hope Department of Entomology at Oxford University. These names are listed below alphabetically, and historical use of each is outlined. We figure those names that were illustrated in Jones and note whether the Jones illustration was referenced in the original description. Although each of these illustrations (Figs. 1, 3, 5, 7, 9, 11) was cited by Fabricius (1793) as being in Jones' Volume 6, they are currently listed in Volume 5 in the Hope Department of Entomology Library title card with a note that they are the same as Volume 6 in Fabricius. Plate and figure numbers are identical in both sources and are cited in the legend for figures 1–12.

Identification of species illustrated by Jones was based primarily upon wing pattern characters. Wing venation, especially the radial veins, usually cannot be seen clearly in Jones' illustrations.

Under Article 23.9.1 of the International Code of



Figs. 1-8. Upperside (left) and underside. 1. *Hesperia anacreon* in Jones' Icones (plate 5, fig. 4). 2. *Satyrium liparops*, female, Atlanta, Georgia. 3. *Hesperia cecrops* in Jones' Icones (plate 21, fig. 2). 4. *Calycopis cecrops*, male neotype, see text for full data. 5. *Hesperia euripides* in Jones' Icones (plate 13, fig. 4). 6. *Parrhasius m-album*, female, Savannah, Georgia. 7. *Papilio mars* in Jones' Icones (plate 18, fig. 2). 8. *Strymon acis*, female, Big Pine Key, Florida. 9. *Hesperia plautus* in Jones' Icones (plate 44. fig. 1). 10. *Callophrys niphon*, male, Alexandria, Virginia. 11. *Hesperia titus* in Jones' Icones (plate 44, fig. 2). 12. *Satyrium titus*, male, Alexandria, Virginia.

Zoological Nomenclature (ICZN 1999), if an older name, such as three of those identified in this paper, was not applied to a species after 1899 and the younger name has been used by at least 10 different authors in 25 works over the past 50 years (but not in less than a 10 year span), then the younger name is to be protected. The references required by this article are cited in the Appendix. Finally, we use ICZN Article 75.3 to propose a neotype to preserve current usage of a name that cannot be identified with certainty from the original description.

RESULTS

1. *Hesperia anacreon* Fabricius, 1793

The illustration in Jones of *Hesperia anacreon*, which was referenced in the original description of Fabricius, is the same species that is currently called *Satyrium liparops* (Clench 1961, Scott 1986) (Figs. 1, 2). The pattern of off-set white lines on the ventral wings of the Jones illustration can refer to no other species in North America (Clench 1961) or elsewhere (Robbins, unpubl.).

Comstock and Huntington (1959: 70) wrote "Neither Butler nor Druce recognized *anacreon*, but it might be determined from Jones' drawings." This name was not recognized in Draudt (1919–1920) or D'Abrera (1993, 1995). There are no known extant types of *H. anacreon* (Druce 1907, Zimsen 1964), and it has not been used as a valid taxon since Westwood (1852). In the Appendix, more than 25 works in which the name *S. liparops* (Le Conte) has been used by more than 10 authors are listed, for which reason this name is now protected.

The names in the synonymy below are clinal geographical forms, but accurately placing the geographical origin of the illustrated specimen of *H. anacreon* F. is likely to be somewhat arbitrary. The synonymy is as follows:

Satyrium liparops (Le Conte, 1833) (*Thecla*), ***nomen protectum,*** type locality: Georgia, USA

Hesperia anacreon Fabricius, 1793 ***nomen oblitum*** (ICZN, Art. 23.9.1) type locality: India

Thecla strigosa Harris, 1862, type locality: Massachusetts, USA

Thecla liparops ab. *pruina* Scudder, 1889, type locality: Massachusetts, USA

Thecla strigosa var. *liparops* Fletcher, 1903, type locality: Manitoba, Canada preoccupied by *Thecla liparops* Le Conte, 1833

Strymon strigosus fletcheri Michener & dos Passos, 1942, replacement name; type locality: Manitoba, Canada

Strymon strigosus aliparops Michener & dos Passos, 1942; type locality: Colorado, USA

Satyrium liparops floridensis Gatrelle, 2001, type locality: Florida, USA

2. *Hesperia cecrops* Fabricius, 1793

Although *Hesperia cecrops* was described from "Indiis", it has been treated as a New World species for more than 125 years, usually as the North American endemic that is currently called *Calycopis cecrops* (Butler 1870, Scudder 1876, Draudt 1919–1920, Holland 1931, Klots 1951, Clench 1961, Field 1967, Howe 1975, Scott 1986, Opler & Malikul 1992, D'Abrera 1993, Glassberg 1999, Fig. 4).

Despite its consistent usage, identification of *Hesperia cecrops* is unclear. Identification of the Jones illustration (Fig. 3)—referenced in the original description of Fabricius—might conceivably refer to one of several species of *Calycopis*. The prominent red basal edging of the postmedian line is consistent with the wing pattern of *C. cecrops* (Figs. 3, 4) as well as with some other *Calycopis* species (Field 1967). The dorsal brown color lacking virtually any blue in the illustration is shared by many "summer form" males of *C. cecrops* (Clench 1961, Field 1967, Scott 1986) (Figs. 3, 4), but occurs occasionally in *C. isobeon* (sometimes referred to by its junior synonym, *C. quintana* [K. Johnson, 1991]). The single ventral hindwing orange-red cubital spot with a small black "pupil" at the basal edge does not exactly match the cubital spot of any *Calycopis*, including *C. cecrops* (Figs. 3, 4). Finally, no publication of which we are aware has ever mentioned a type specimen nor is an extant type known (Zimsen 1964).

We designate a male neotype for *Hesperia cecrops* Fabricius, 1793 following the qualifying conditions of ICZN Article 75.3. The reason for designating the neotype is to conserve usage of this name as it has been employed almost exclusively for more than a century (Scudder 1876, Draudt 1919-1920, Holland 1931, Klots 1951, Clench 1961, Field 1967, Howe 1975, Scott 1986, Opler & Malikul 1992, D'Abrera 1993, Glassberg 1999). *Hesperia cecrops* is differentiated from its close relatives by the characters given in Field (1967). The neotype male (Fig. 4) has one white label [Savannah, GEORGIA/ Chatham County/ 30 May '64/ Coll by S.S. Nicolay] with all lines printed except for the handwritten date. We have added a printed red neotype label [NEOTYPE/ *Hesperia cecrops* Fabricius/ Robbins & Lamas, 2006]. As noted, no extant type is known (Zimsen 1964). The neotype wing pattern is similar to the figure in Jones (Figs. 3, 4) and is consistent with usage of this name. The original type locality was erroneous, and the new type locality for

Hesperia cecrops Fabricius, 1793 is Savannah, Georgia, USA in accordance with ICZN Article 76.3. The neotype is deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA.

3. *Hesperia columella* Fabricius, 1793

Jones' Icones was not referenced in the original description of *H. columella* nor did Jones illustrate it. However, Robbins examined the two extant syntypes of *H. columella* in Copenhagen (Zimsen 1964, one had been at Kiel) and illustrated one of them (Robbins & Nicolay 1999). Although this name had been applied to the species now called *Strymon istapa* (Reakirt) (Riley 1975, Smith et al. 1994), which occurs from the southern United States to Brazil and Peru, it actually refers to a species endemic to the Lesser Antilles (Robbins & Nicolay 1999).

4. *Hesperia euripides* Fabricius, 1793

The illustration in Jones of *Hesperia euripides*, which was referenced in the original description of Fabricius, is the same species that is currently called *Parrhasius m-album* (Boisduval & Le Conte) (Nicolay 1979) (Figs. 5, 6). *Parrhasius m-album* differs from *P. moctezuma* Clench, *P. urraca* Nicolay, and *P. selika* (Hewitson) (= *P. appula* [Hewitson], Robbins 2004) by lacking both ventral forewing submarginal lines (one may be vestigial) (Nicolay 1979) and lacking virtually all red on the ventral hindwing anal lobe. The illustration of *H. euripides* has both characters of *P. m-album* (Figs. 5, 6). There are no known extant types of *H. euripides* (Zimsen 1964), and it was last "used" as a valid species by Butler (1870) and Kirby (1871). It was not mentioned by Draudt (1919–1920) or D'Abrera (1993, 1995). In the Appendix, more than 25 works in which the name *P. m-album* (Boisduval & Le Conte) has been used by more than 10 authors are listed. All conditions of Article 23.9.1 are met, for which reason prevailing usage is to be maintained.

Parrhasius m-album (Boisduval & Le Conte, 1833)(*Thecla*), ***nomen protectum***; type locality: Georgia, USA

Hesperia euripides Fabricius, 1793 ***nomen oblitum*** (ICZN, Art. 23.9.1); type locality: Indiis

Thecla psyche Boisduval & Le Conte, 1833, type locality: Georgia, USA

5. *Papilio ixion* Fabricius, 1775

Papilio ixion was described from "in India," but no figure of this species was referenced nor is a type specimen known to be extant (Zimsen 1964). This name has been treated as a junior synonym of the species now called *Strymon acis* (Drury) (Fabricius 1793, Godart 1824, Westwood 1852) and as a senior synonym of the species now called *Parrhasius m-album* (Butler 1870, Kirby 1871), but reasons have not been given for either synonymy. Comstock and Huntington (1961: 240) wrote "We cannot identify *ixion*." Robbins (2004) treated it as a *nomen dubium*. Without substantive new information, continuing *nomen dubium* status preserves nomenclatural stability.

6. *Papilio mars* Fabricius, 1776

Fabricius (1793) synonymized this name from "America meridionali" with *Papilio ixion* F. and *Papilio acis* Drury, 1773 (identification of *acis* from the original illustration is definitive even though the type locality of "New York" is incorrect). The latter synonymy has been used ever since although no types are known to be extant (Zimsen 1964). Jones illustrated *P. mars*, which is the species now called *Strymon acis* (Drury) (Figs. 7, 8). This information is consistent with current usage, and identification of the name is stable.

7. *Hesperia plautus* Fabricius, 1793

The illustration in Jones of *Hesperia plautus*, which was referenced in the original description of Fabricius, is the same species that is currently called *Callophrys (Incisalia) niphon* (Clench 1961, Scott 1986) (Figs. 9, 10). Its ventral forewing possesses two transverse bars in the discal cell and its hindwing costa is straight, which differentiates it from *C. eryphon* (Boisduval) and *C. lanoraieensis* (Sheppard) (Clench 1961). There are no known extant types of *H. plautus* (Zimsen 1964).

Kirby (1879) listed *Thecla niphon* (Hübner) as a synonym of *Thecla plautus* (Fabricius), but this action was apparently overlooked. Comstock and Huntington (1962: 116) wrote "Scudder places *plautus* in the synonymy of *niphon* Hübner based on Abbot's unpublished drawing in the British Museum. He credited the name *plautus* to Abbot and not to Fabricius. Fabricius gave a reference to Jones' figure '6, tab. 44. fig. 1.' His description reads like *niphon* Hübner. The date of *plautus* is 1793; the date of *niphon* is 1823. This should be investigated for possible synonymy."

Because Scudder incorrectly attributed *plautus* to John Abbot, *plautus* Scudder is a *nomen nudum*. The name *plautus* F. has not been used as a valid taxon since 1879. In the Appendix, more than 25 works in which the name *C. (I.) niphon* (Hübner, [1819]) has been used by more than 10 authors are listed. All conditions of Article 23.9.1 are met. Despite the synonymy in Kirby (1879) and the discussion in Comstock and Huntington

(1962), the name *Lycus niphon* Hübner is protected.

Callophrys (*Incisalia*) *niphon* (Hübner, [1819]) (*Lycus*), ***nomen protectum***, type locality: [Georgia], USA

Hesperia plautus Fabricius, 1793 ***nomen oblitum*** (ICZN, Art. 23.9.1); type locality: Indiis

Papilio plautus Scudder, 1876 ***nomen nudum***, type locality: Georgia, USA

Incisalia niphon var. *clarki* T.N. Freeman, 1938, type locality: Ontario, Canada

8. *Hesperia titus* Fabricius, 1793

The identification of this species has been clear since it was described from "Anglia." The original description references an illustration in Jones (Fig. 11) that is consistent with the current identification of *Satyrium titus* (Fig. 12) (Clench 1961, Scott 1986). No extant types are known (Zimsen 1964), but Butler (1870) suggested that a specimen in the Natural History Museum (London) might be a type from the Drury collection. It is also consistent with the current identification of *Satyrium titus*. The name *titus* F. was involved in a ruling on generic names, and was placed on the Official List of Specific Names in Zoology as name #1605 (ICZN 1959).

DISCUSSION

The nomenclature of North American Eumaeini has been markedly stabilized in the past few years. Application was made to, and granted by, the International Commission on Zoological Nomenclature to protect the name *Ministrymon azia* (Hewitson) from an older name (Robbins & Lamas 2004, ICZN 2006). The nomenclatural confusion between *Strymon yojoa* (Reakirt) and *S. daraba* (Hewitson) has been untangled so that the former name still applies to the species that ranges into the United States (Robbins & Lamas 2002). The taxonomic confusion between *Strymon columella* (Fabricius) and *S. istapa* (Reakirt) has been straightened out so that the former name no longer applies to the North American fauna. Three widely used names, *P. m-album*, *C. (I.) niphon*, and *S. liparops*, have now been protected from older Fabrician names that have not been used in over a century. Finally, a neotype for *Hesperia cecrops* Fabricius stabilizes this name as it has been used consistently for over a century.

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LITERATURE CITED

BUTLER, A. G. 1870. Catalogue of diurnal Lepidoptera described by Fabricius in the collection of the British Museum. Taylor & Francis, London, 303 pp. + 3 pl.

CLENCH, H. K. 1961. Tribe Theclini. pp. 177–220. *In* P. R. Ehrlich & A. H. Ehrlich (eds.) How to know the butterflies, , Brown Company, Dubuque, 262 pp., 525 figs.

COMSTOCK, W. P. & E. I. Huntington. 1959. An annotated list of the Lycaenidae (Lepidoptera: Rhopalocera) of the Western Hemisphere. J. N. Y. Entomol. Soc. 67(2): 59–95.

——. 1962. An annotated list of the Lycaenidae (Lepidoptera: Rhopalocera) of the Western Hemisphere. J. N. Y. Entomol. Soc. 70(2): 100–118.

D'ABRERA, B. 1993. Butterflies of the Holarctic Region. Part III. Nymphalidae (concl.), Libytheidae, Riodinidae & Lycaenidae. Hill House, Victoria, pp. 336–524.

D'ABRERA, B. 1995. Butterflies of the Neotropical Region. Part VII. Lycaenidae. Hill House, Victoria, pp. 1098–1270.

DRAUDT, M. 1919-1920. Theclini F. pp. 744–812. *In* A. Seitz (Ed.) Macrolepidoptera of the World, vol. V, The American Rhopalocera, , Alfred Kernen Verlag, Stuttgart, 1140 pp., 194 pls.

DRUCE, H. H. 1907. On neotropical Lycaenidae, with descriptions of new species. Proc. Zool. Soc. Lond. 1907(3): 566–632, 6 plates.

FABRICIUS, J. C. 1793. Entomologia systematica emendata et aucta, etc. C. G. Proft, fil. et soc., Hafniae, vol. 3, 488 pp.

FIELD, W. D. 1967. Preliminary revision of butterflies of the genus *Calycopis* Scudder (Lycaenidae: Theclinae). Proc. U. S. Natl. Mus. 119 (3552): 1–48.

GLASSBERG, J. 1999. Butterflies through binoculars. The East. Oxford University Press, New York, x + 242 pp.

GODART, J. B. 1824. pp. 329–706, 708–711, 794-828. *In* Latreille, P. A. & J. B. Godart, Encyclopédie Méthodique. Histoire naturelle. Entomologie, ou histoire naturelle des crustacés, des arachnides et des insectes. Veuve Agasse, Paris, 9(2): 329–828

HOLLAND, W. J. 1931. The Butterfly Book. New and Thoroughly Revised Edition. A Popular and Scientific Manual, Describing and Depicting all the Butterflies of the United States and Canada. New York, Doubleday, Doran & Company, Inc. xii + 424 pp., 77 pls., 198 figs.

HOWE, W.H. 1975. The butterflies of North America. Doubleday & Company, Inc., New York, xiii + 633 pp.

HÜBNER, J. 1819. Verzeichniss bekannter Schmettlinge [sic]. Jacob Hübner, Augsburg, (2-8): 17– 128.

ICZN. 1959. Opinion 541. Suppression under the plenary powers of the generic names "*Chrysophanus*" Hübner, 1818, and "*Bithys*" Hübner, 1818, (Class Insecta, Order Lepidoptera) ("Opinion" supplementary to "Opinion" 165). Opin. Decl. Int. Comm. Zool. Nomen. 20(8): 87–101.

——. 1999. International Code of Zoological Nomenclature, Fourth Edition. International Trust for Zoological Nomenclature, London, xxix + 306 pp.

——. 2006. Opinion 2144 (Case 3282). *Thecla azia* Hewitson, 1873 (Insecta, Lepidoptera): specific name conserved. Bull. Zool. Nomen. 63 (1): 76-77.

KIRBY, W.F. 1871. A synonymic catalogue of diurnal Lepidoptera. John Van Voorst, London, vii + 690 pp.

——. 1879. Catalogue of the collection of diurnal Lepidoptera formed by the late William Chapman Hewitson of Oatlands, Walton-on-Thames; and bequeathed by him to the British Museum. John Van Voorst, London, iv + 246 pp.

KLOTS, A. B. 1951. A field guide to the butterflies of North America, east of the Great Plains. Houghton Mifflin, Boston, 349 pp.

LAMAS, G. 1979. The Ithomiinae represented in Jones' unpublished "Icones", and the identity of the Fabrician species *Papilio hyalinus* and *obscuratus* (Lepidoptera, Nymphalidae). Brenesia 16: 101–106.

NICOLAY, S. S. 1979. Studies in the genera of American hairstreaks. 5. A review of the Hubnerian genus *Parrhasius* and description of a new genus *Michaelus* (Lycaenidae: Eumaeini). Bull. Allyn Mus. 56: 1-51.

OPLER, P.A. & V. MALIKUL. 1992. A field guide to Eastern butterflies. Houghton Mifflin Company, Boston, xix + 396 pp.

RILEY, N. D. 1975. A field guide to the butterflies of the West Indies. Collins, London. 224 pp.

ROBBINS, R. K. 2004. Lycaenidae. Theclinae. Tribe Eumaeini, pp. 118–137. in: Checklist: Part 4A. Hesperioidea - *Papilio*noidea, Lamas, G. (Ed.), in: Atlas of Neotropical Lepidoptera, Heppner, J. B. (Ed.),. Volume 5A. Association for Tropical Lepidoptera; Scientific Publishers, Gainesville.

——. & M. DUARTE. 2005. Phylogenetic analysis of *Cyanophrys* Clench, a synopsis of its species, and the potentially threatened *C. bertha* (Jones) (Lycaenidae: Theclinae: Eumaeini). Proc. Entomol. Soc. Washington 107(2): 398–416.

——. & G. LAMAS. 2002. Nomenclatural Changes in the Neotropical Eumaeini (Lepidoptera: Lycaenidae: Theclinae). Revta bras. Zool. 19(Supl. 1): 197–214.

——. 2004. *Thecla azia* Hewitson, 1873 (Insecta, Lepidoptera): proposed conservation of the specific name (Case 3282). Bull. Zool. Nomen. 61(2): 98–99.

——. & S. S. NICOLAY. 1999. Taxonomy and nomenclature of *Strymon istapa* and *S. columella* (Lycaenidae: Theclinae). J. Lepid. Soc. 52(3): 318–327.

SCOTT, J. A. 1986. The butterflies of North America, a natural history and field guide. Stanford University Press, Stanford, 583 pp.

SCUDDER, S. H. 1876. Synonymic list of the butterflies of North America, north of Mexico, part II. Rurales. Bull. Buffalo Soc. Natur. Sci. 3: 98–104, 105–129.

SMITH, A.Z. 1986. A history of the Hope Entomological Collections in the University Museum, Oxford with lists of Archives and Collections. Clarendon Press, Oxford, xiii + 172 pp.

SMITH, D.S., L.D. MILLER & J.Y. MILLER. 1994. The butterflies of the West Indies and South Florida. Oxford University Press, Oxford, x + 264 pp.

WESTWOOD, J.O. 1852. pp. 251–534 in The genera of diurnal Lepidoptera: comprising their generic characters, a notice of their habits and transformations, and a catalogue of the species of each genus, Vol. 2, Doubleday, E. (Ed.). Longman, Brown, Green & Longmans, London.

ZIMSEN, E. 1964. The type material of I. C. Fabricius. Munksgaard, Copenhagen, 656 pp.

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APPENDIX

Twenty-six references in the past 50 years by 42 authors in which the names *Thecla liparops* Le Conte, 1833, *Thecla m-album* Boisduval & Le Conte, 1833, and *Lycus niphon* Hübner, [1819] have been used. ° Three additional references using *Thecla liparops* Le Conte, 1833 and Lycus *niphon* Hübner, [1819]. °° Three additional references using *Thecla m-album* Boisduval & Le Conte, 1833.

° BIRD, C. D. 1995. Alberta butterflies. Edmonton Provincial Museum of Alberta, Edmonton. 349 pp.

CASSIE, B, J. GLASSBERG, P. OPLER, R. ROBBINS, AND G. TUDOR. 1995. North American Butterfly Association (NABA) Checklist & English Names of North American Butterflies, First Edition. North American Butterfly Association, Morristown, New Jersey. 43 pp.

CLENCH, H. K. 1961 (see lit. cited).

°°——. 1962. *Panthiades m-album* (Lycaenidae): remarks on its early stages and on its occurrence in Pennsylvania. J. Lepid. Soc. 15: 226–232.

COVELL, C. W. 1999. The butterflies and moths (Lepidoptera) of Kentucky: an annotated checklist. Scientific and Technical Series (State Nature Preserves Commission), No. 6, 220 pp.

D'ABRERA, B. 1993 (see lit. cited).

DOS PASSOS, C. F. 1964. A synonymic list of the Nearctic Rhopalocera. Mem. Lepid. Soc., No. 1, 145 pp.

FORBES, W. T. M. 1960. Lepidoptera of New York and neighboring states, Agaristidae through Nymphalidae including butterflies. Part IV. Cornell Univ. Agricul. Station, New York State College of Agriculture, Memoir 371, 188 pp.

GLASSBERG, J. 1993. Butterflies through binoculars. A field guide to butterflies in the Boston - New York - Washington region. Oxford University Press, New York, 160 pp. 40 pls.

GLASSBERG, J. 1999. (see lit. cited).

GLASSBERG, J., M. C. MINNO & J. V. CALHOUN. 2000. Butterflies through binoculars. A field, finding, and gardening guide to butterflies in Florida. Oxford University Press, New York, viii + 242p.

GOCHFIELD, M. & J. BURGER. 1997. Butterflies of New Jersey: a guide to their status, distribution, conservation, and appreciation. Rutgers University Press, New Brunswick. 327 pp.

HARRIS, L. 1972. Butterflies of Georgia. University of Oklahoma Press, Norman. 326 pp.

HEITZMAN, J. R. 1987. Butterflies and moths of Missouri. Missouri Dept. of Conservation, Jefferson City. 385 pp.

HOWE, W.H. 1975. (see lit. cited).

IFTNER, D. C., J. A. SHUEY, & J. V. CALHOUN. 1992. Butterflies and skippers of Ohio. Ohio Biol. Surv. Bull. New Ser. 9:1–212.

—— & D. M. Wright. 1996. Atlas of New Jersey butterflies. Special Private Publication, Sparta. 28 pp.

° KLASSEN, P., A. R. WESTWOOD, W. B. PRESTON, & W. B. MCKILLOP. 1989. The butterflies of Manitoba. Manitoba Museum of Man and Nature, Winnipeg. 290 pp.

° LAYBERRY, R. A., P. W. HALL, & J. D. LAFONTAINE. 1998. The butterflies of Canada. University of Toronto Press, Toronto. 280 pp.

MILLER, J.Y. 1992. The common names of North American butterflies. Smithsonian Institution Press, Washington, D.C., ix + 177p.

MILLER, L. D. & F. M. BROWN. 1981. A catalogue/checklist of the butterflies of America north of Mexico. Lepid. Soc. Mem. No. 2. 280 pp.

°° NICOLAY, S. S. 1979. (see lit. cited).

OPLER, P.A. & G.O. KRIZEK. 1984. Butterflies East of the Great Plains. An illustrated natural history. Johns Hopkins University Press, Baltimore, xvii + 294 pp.

OPLER, P.A. & V. MALIKUL. 1992. (see lit. cited).

PYLE, R. M. 1981. The Audubon Society field guide to North American butterflies. Alfred A. Knopf, New York. 924 pp.

SCOTT, J. A. 1986 (see lit. cited).

SHAPIRO, A. M. 1974. Butterflies and skippers of New York State. Search Agriculture, Entomology (Ithaca) 12.

SHAPIRO, A. M. 1966. Butterflies of the Delaware Valley. American Entomological Society, 79 pp.

SHULL, E. M. 1987. The butterflies of Indiana. Indiana Academy of Science, Bloomington, 262 pp.

°° SMITH, D. S., L. D. MILLER, & J. Y. MILLER. 1994. The butterflies of the West Indies and South Florida. Oxford University Press. Oxford, 264 pp.

TIETZ, H. M. 1972. An index to the described life histories, early stages and hosts of the Macrolepidoptera of the continental United States and Canada. Vol. 1. Allyn Museum of Entomology, Sarasota, 536 pp.

ZIEGLER, J. B. 1960. Preliminary contribution to a redefinition of the genera of North American hairstreaks (Lycaenidae) north of Mexico. J. Lepid. Soc. 14: 19–23.

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COSMOCLOSTIS AGLAODESMA: DESCRIPTION OF THE LARVA AND PUPA (PTEROPHORIDAE: PTEROPHORINAE: PTEROPHORINI)

Additional key words: morphology, characters, immature stages, tribal placement, Australia

The genus *Cosmoclostis* Meyrick includes 12 species: 3 Australasian, 3 Afrotropical, and 6 Oriental in distribution (Fletcher 1947, Gielis 2003, Hao et al. 2004). Hostplants have been reported for 4 species (Hao et al. 2004, Matthews & Lott 2005) but the immature stages are poorly known. Fletcher (1932) illustrated and briefly described the larva and pupa of *C. pesseuta* Meyrick (as *C. premnicola* Fletcher). We describe and illustrate the pupa and a late instar larva of the type species, *C. aglaodesma* Meyrick, using setal nomenclature following Stehr (1987) and Heinrich (1916). Arenberger (1998) illustrates the adult and genitalia of this species.

Cosmoclostis aglaodesma occurs along the Pacific Rim of Australia. Meyrick's (1886) holotype is from Sydney, New South Wales. This species has also been collected in Toowong, Queensland (Arenberger 1998) and further north from Iron Range (see material examined). The larval host genus of these Iron Range specimens is *Gmelina* (Lamiaceae) but the species is not indicated on the label. Fletcher (1931) listed *G. arborea* Roxb. as the host for *C. aglaodesma* from Assam, India, but according to Arenberger (1998), *C. aglaodesma* is restricted to Australia and these records are based on misdetermined specimens. *Gmelina arborea* is the host for *C. leucomochla* Fletcher in India (Nair 2001) and *C. gmelina* Hao, Li, & Wu in China (Hao et al. 2004). *Gmelina moluccana* Backer ex K. Heyne is the host for *C. lamprosema* Fletcher in the Solomon Islands (Arenberger 1998).

Material examined. Australia: Queensland: Iron Range 19 March 1964 I.B.F. Common & M.S. Upton, on *Gmelina* sp. (1 larva, 1 pupa) [Australian National Insect Collection]. Specimens identified by I.B.F. Common.

Larva. Figures 1a–c, 2a–d. Length 8 mm, maximum width 2.5 mm (excluding setae). Three forms of setae present: simple, with smooth shaft and pointed apex; spiculate with pointed or blunt apex; and scaliform. Dorsal and subdorsal setae reduced, minute and closely appressed to body. Lateral setae on prominent flange verrucae with dorsal-most setae radiating in a single plane forming conspicuous lateral fringe. Lateral setae short to long, longest setae 1.73 mm or 0.7× maximum body width.

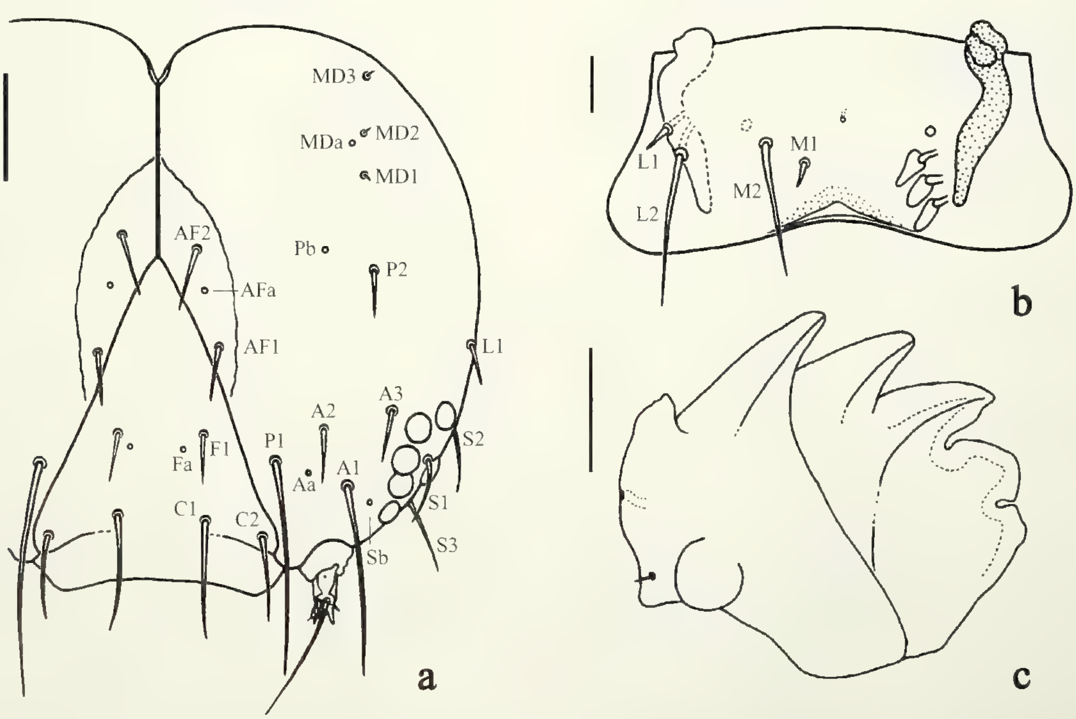

FIG. 1. Larval head of *Cosmoclostis aglaodesma*: **a**, Frontal view of cranium, scale line = 0.125 mm; **b**, Labrum, epipharyngeal surface on right, scale line = 0.035 mm; **c**, Right mandible, scale line = 0.040 mm.

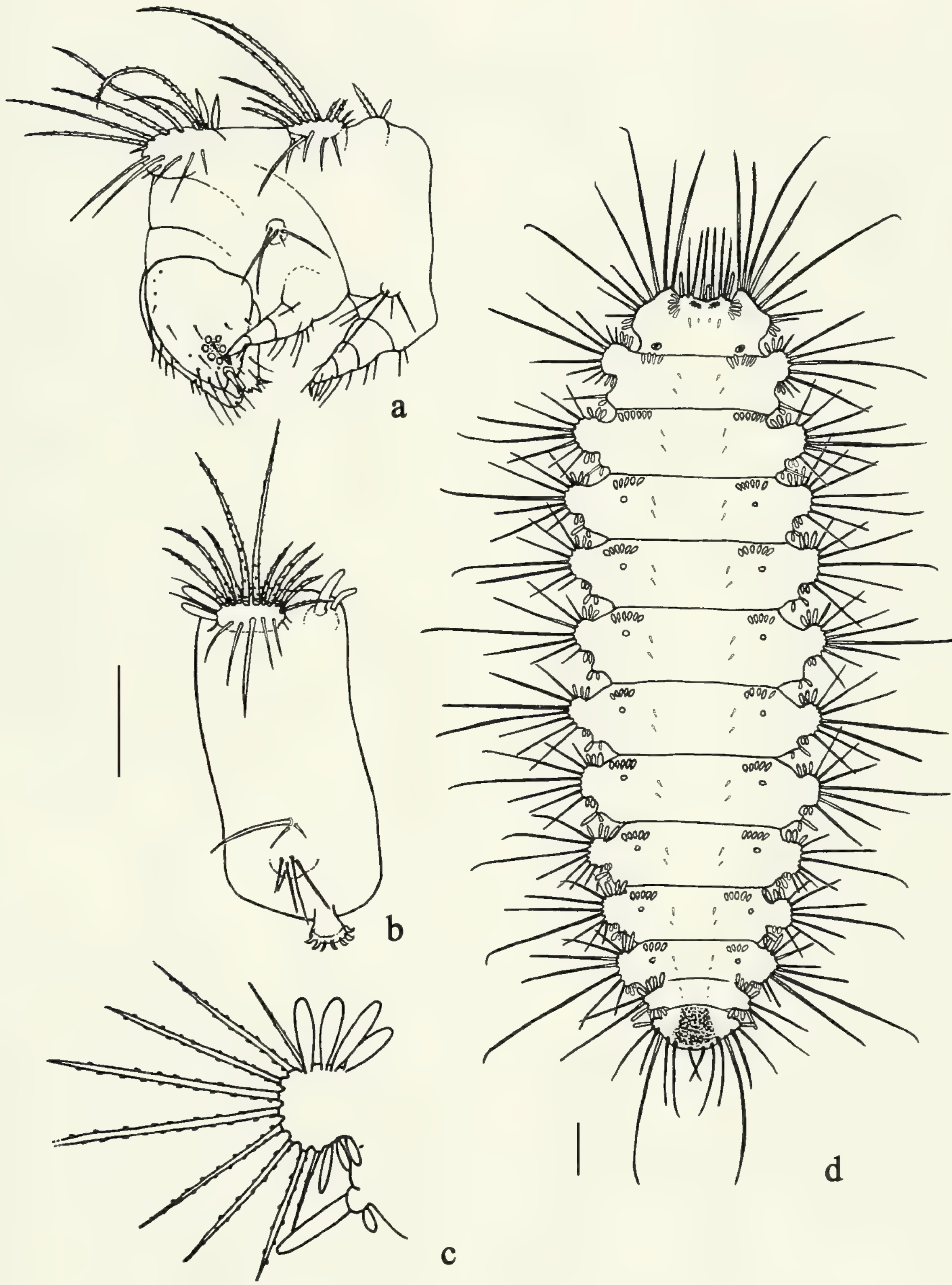

FIG. 2. *Cosmoclostis aglaodesma* larva: **a**, lateral view of head, prothorax, and mesothorax; **b**, lateral view of segment A3, scale line = 0.5 mm; **c**, morphological detail of lateral setae on abdomen, dorsal view; **d**, larva, dorsal view, scale line = 1.0 mm.

Head. Hypognathous. Anterior aspect round. Width 0.74 mm. Adfrontal sclerite not reaching anteclypeus. Pore AFa present. Lateral adfrontal suture length about 1.3× clypeal width, just exceeding 1.5× epicranial suture length. Setae AF1, AF2, F1, A2, A3, P2, L1, S1, and S2 about 0.25× clypeal width. Seta C1 about 0.5× clypeal width; C2 and S3 just less than 0.5× clypeal width. Length of setae P1 and A1 just less than 1× clypeal width, P1 slightly longer than A1. Seta P2 and pore Pb laterad of AF2. Seta P1 unusually distant from P2, more ventrally placed than in other pterophorid genera, about midway between F1 and A1. Pore Aa between P1 and A1. Seta A2 dorsad of pore Aa. Labrum with 4 setae; length of M2 and L2 about 0.25× clypeal width, that of M1 and L1 less than 0.2× M2 or L2. Labrum distally flared, without conspicuous notch, ventral margin slightly concave. Three epipharyngeal setae present. Mandible 6-toothed; ventral tooth distinctly basad of adjacent tooth and not arising from the same ridge (ventral tooth apex about midway between condyle and apex of adjacent tooth). Mandible width slightly greater than length; distal seta replaced by pore, proximal seta close to condyle, length about 0.3× condyle diameter.

Thorax. Dorsum of prothorax with setae XD1, XD2, SD1, and SD2 approximate and transversally aligned as anteriorly projecting fringe along anterior margin. Seta XD1 and XD2 similar in length, about 0.72 mm. Length of seta SD1 slightly less than that of XD2, SD2 about 0.3× XD2. A smooth scaliform secondary seta present between midline and XD1, length just less than SD2. With diffuse lightly sclerotized patch posteriad of XD setae. With cluster of 5 minute scaliform setae posteriad of SD2; setae directed laterad, closely appressed to body. Setae D1 and D2 minute and obscure, D1 less than 0.03 mm; D2 about 0.6 mm, laterad and slightly posteriad of D1, directed anteriad, appressed to body. Lateral verruca oblong, projecting anteriad of central anterior margin. Distal margin of verruca with 9 short to long spiculate setae flanked by 3-5 short to minute scaliform setae anteriad and 2 minute scaliform setae posteriad. Ventral surface of verruca with 8-10 additional minute to medium length setae projecting ventrad. Prothoracic spiracle on T1 dorsum laterad near posterior segment margin, round, not exserted, peritreme light. Subventral verruca small, round, scarcely elevated, with 3 short simple setae and 1 or 2 minute setae.

Segments T2–T3 with D setae obscure, minute; D2 posteriad of D1, both directed anteriad, appressed to body. Primary seta SD1 apparently absent, with verruca remnant of 4–6 minute secondary scaliform setae along anterior margin dorsad of L verruca. Fan of about 9 short to long spiculate setae present on flange type L verruca; setae projecting laterad in single plane, about 3 minute scaliform setae anteriad on verruca and 2 posteriad. About 5 minute to medium length simple setae on ventral surface of L verruca. A small tubercle present at lateral margin posteriad of main L (L1+L2) verruca with central short, articulated spiculate seta (L3) and minute secondary scaliform seta posteriad on tubercle. Subventral verruca as on T1.

Abdomen. Segments A1–A8 with D1 and D2 as on T2–T3. Primary seta SD1 absent. A transverse row of 4-6 scaliform secondary setae along anterior margin anteriad of spiracle. Spiracles inconspicuous, round, peritremes light. Main lateral verruca as on T2–T3. Tubercle posteriad of main L verruca with 2 secondary setae; apical seta short (about 0.24 mm), scaliform; not spiculate or articulated at base as on T2–T3. Seta posteriad on tubercle minute, scaliform. Tubercle and associated setae absent on A8. Seta L3 of medium length, up to 0.38 mm, simple, central on small verruca with 2–3 minute setae; longitudinally aligned with SV verruca on T2–T3. Subventral verruca small, round, with 3–5 short to minute simple setae. Prolegs on A3–A6 with length about 2× width; 7–8 crochets arranged in mesopenellipse. Prolegs placed very close to meson, distance between right and left proleg less than proleg diameter. Seta V1 minute, solitary on all segments, mesad at proleg base on A3–A6.

Segment A9 with setae D1 and D2 as on A8 but shorter. Lateral verruca smaller, with only 2 spiculate setae (L1 & L2) and 5–6 scaliform setae anteriad, 3–4 posteriad. Longest of 2 spiculate setae (L2, posteriad) 0.48 mm. One short simple seta on ventral surface of verruca. Seta L3 absent. Subventral verruca with 3 minute to short setae, verruca positioned more laterad than SV verruca of A8. Anal plate (A10) with D1 setae apparently absent. Minute, thin simple seta, possibly D2, positioned just anteriad of fringe setae on caudal margin. Dorsum of anal plate with moderately sclerotized longitudinal band on central third from anterior margin to caudal margin, flared toward caudal margin to include bases of 3 dorsal-most caudal setae. Caudal margin rounded, with 7 short to long spiculate setae; 2 most anterior setae arising from lateral tubercle. Two minute scaliform setae anteriad on lateral tubercle. Ventral rim of anal plate with about 9 minute to short simple setae. Anal proleg with 9 crochets in transverse arc. About 6 short to minute setae projecting posteriad from posterior side of proleg.

Pupa. Figure 3a–c. Length 9 mm, maximum width 3 mm (includes verruca bases but not setae). Primary and secondary setae present, minute to medium in length. Longest setae, SD1 and SD2 on T1, and L setae on lateral verrucae of abdomen, reaching 0.6 mm or 0.2× maximum body width. Primary D setae minute, appressed, blunt-tipped or scaliform, remaining primary and secondary setae simple or minutely spiculate. Dorsum with localized hyaline scobinations present. Head and thorax with prominent flanges bearing marginal setal fringe. Lateral verrucae prominent plate-like flanges on abdominal segments. Dorsal aspect with wings hidden by flanges and setae. Thoracic appendages without secondary setae.

Head. Dorsum with vertex distinguishable as triangular sclerite mediad of antennal bases. Front produced as prominent bilobed flange. Dorsum of front without setae, lateral margin of each flange lobe bearing fringe of 10–11 minute to short setae; primary setae AF1 and AF2 distinguishable from adjacent secondary setae as being longer, more distinctly spiculate, and by having articulated bases. Ventral surface of front smooth, without secondary setae. Seta F1 simple, about 0.24 mm, projecting laterad near anterior extent of gena. Frontoclypeal suture indistinct. One minute, thin, clypeal seta (C2) present, length about 0.5× F1, directed posteriad. Pilifers distinct, separated by labial palpus at meson. Genal seta slightly longer than C2. Suture between gena and smooth eye barely discernible. Juncture of smooth and sculptured eye also obscure. Sculptured eye with two minute setae present, lengths similar to genal seta. Maxilla with base just exceeding 0.5× T2 leg length, reaching A3; mid section partly concealed by T1 leg, distal tip exposed between T2 leg tips, even or just exceeding T2 leg apex. Antenna extending along T2 leg to point midway between T1 and T2 leg tips, not exceeding forewing. Antenna without setae except for 3 short secondary setae along flange at base. Setae and flange visible in both dorsal and ventral aspects.

Thorax. Pronotum constricted at midline, with prominent rounded flange laterad bearing marginal fringe of 14–16 minute to short setae. Secondary fringe setae reaching 0.38 mm in length. Primary setae SD1 and SD2 most posterior of fringe setae, up to 0.55 mm in length, more spiculate than preceding setae, bases articulated. Setae D1 and D2 minute, less than 0.12 mm long, scaliform, directed anteriad, appressed. Seta D2 posterolateral of D1. Prothoracic spiracle embedded in T2 margin, not elevated, peritreme light. Fore leg with coxa/trochanter exposed as sclerite between maxilla base and tibia/tarsal sclerite. Fore leg apex reaching A4 posterior margin.

Dorsum of mesothorax relatively flat, without dorsal ridges or keel. Setae D1 and D2 minute (0.14 mm long), scaliform to blunt-tipped, appressed. Seta D1 directed anteriad, D2 posteriad of D1, directed laterad. Numerous hyaline scobinations present near D setae. Primary SD setae absent. Lateral margin with bilobed flange. Anterior lobe small, with arc of about 6 minute blunt-tipped secondary setae at margin, continued anteriad by transverse row of about 4 setal bumps or scobinations, posteriad by about 5 microscopic scaliform setae. Posterior flange lobe broadly rounded, with marginal fringe of up to 14 minute blunt-tipped secondary setae. Forewing and mid leg apex reaching A5 posterior margin.

Metathorax with D setae as on T2 but closer to anterior margin. Hyaline scobinations present. Subdorsal setae absent. Lateral flange broadly rounded, not subdivided; with marginal fringe of 18-19 minute to short setae. Hindwing not visible in dorsal aspect, reaching A2 posterior margin in lateral aspect. Hind leg concealed beneath T2

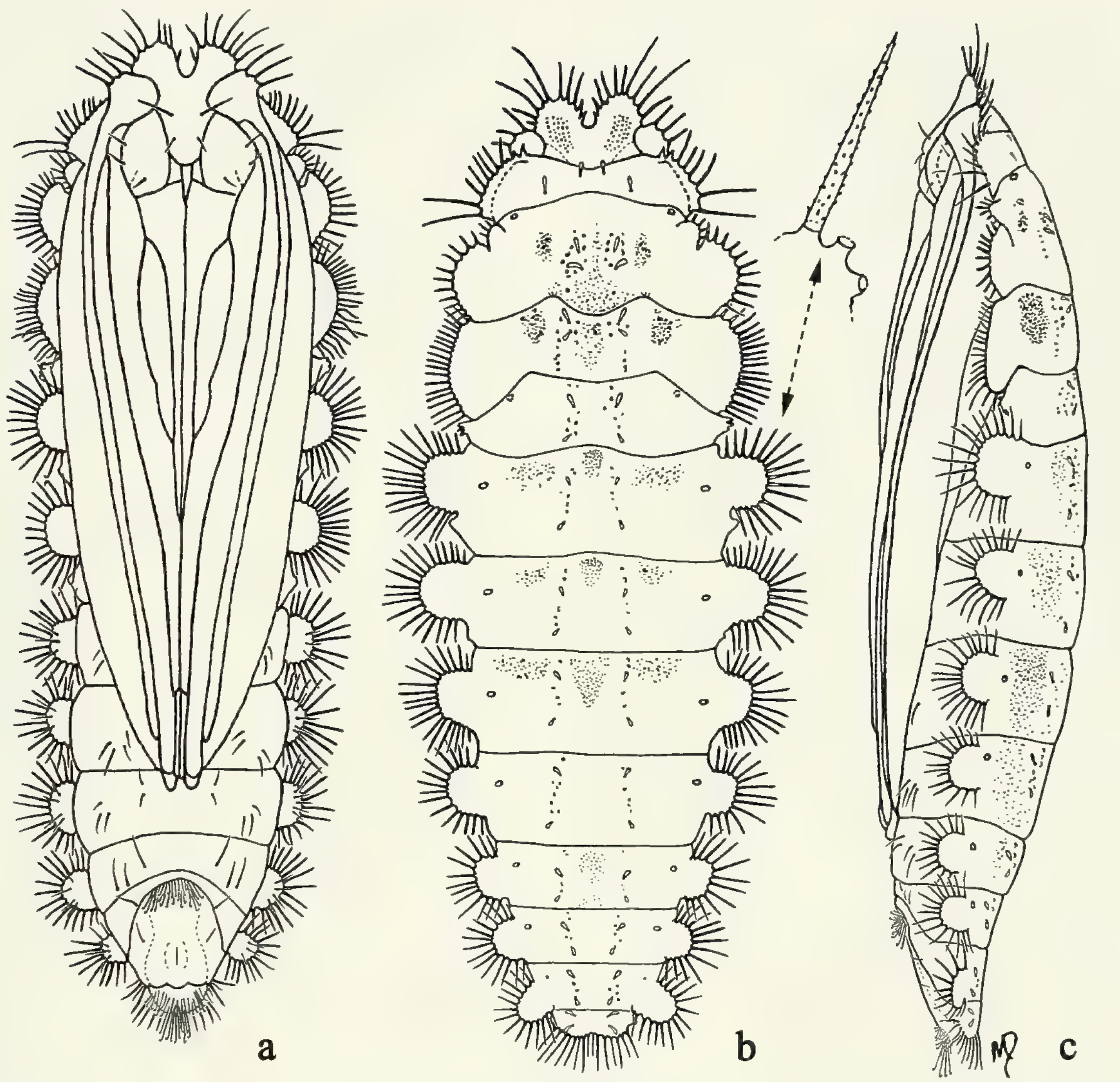

FIG. 3. *Cosmoclostis aglaodesma* pupa: **a**, ventral view; **b**, dorsal view with enlargement showing structural detail of a spiculate lateral seta; **c**, lateral view. scale line = 1.0 mm.

leg, exposed tips just exceeding T2 leg and apex of maxilla.

Abdomen. Segments A1–A8 with D setae generally as on T1–T2 but spaced apart at about 0.3× and 0.6× from anterior margin, seta D2 directed posteriad instead of laterad. Scobinations associated with D setae arranged in longitudinal row. Subdorsal setae apparently absent. Spiracle on A1 non-functional, visible beneath cuticle at anterolateral margin (concealed by hindwing in most pterophorid genera). Spiracles functional on A2–A7, peritremes light, elevated just above surface on A2. Spiracular scar remnant present on A8. Lateral flange verruca present on A2–A8 but absent on A1. Flange verrucae conspicuous, plate or paddle-like, projecting from side of each segment, size gradually decreasing on posterior segments. Fan of up to 20 minute to short setae present along verrucae margins. Longest setae just exceeding verruca diameter. Setae minutely spiculate. Segments A4-A8 with 3-5 minute simple setae on ventral surface of verruca. Small tubercle bearing series of about 3 small bumps or scobinations present on A1–A2, bump single on A3. Tubercle apical on A1, posteriad of L verruca on A2–A3. Venter of segments A4–A7 with cluster of 2–3 minute, simple setae in L3 position (absent on A8); setae directed posteriad on A4–A6, anteriad on A7. Segments A5–A6 with 2 minute, simple SV setae, A7 with 1 SV seta; SV setae erect on A5–A6, directed anteriad on A7. Segment A8 with 1 SV seta near A8/A9 margin

Segment A9 with setae D1 and D2 approximate, minute, with few adjacent hyaline scobinations. Posterior margin of A9 terminal in dorsal aspect, with middorsal indentation; 8 short, minutely spiculate setae (each side) forming caudal fringe. Dorsum of segment A10 reduced to small narrow rim, subterminal, beneath overriding A9 posterior margin. Venter of A9/10 fused. One minute SV seta present on A9. Anterior and posterior hooked hamuli present. Anterior hamuli patch dense, longest hamuli laterally placed. Posterior hamuli with central tuft of about 12 longer (0.36 mm) hamuli flanked by dense patch of shorter hamuli.

We have examined early instar larvae of *C. leucomochla* from Kerala State, India. They were

generally very similar to those of *C. aglaodesma* and shared certain characters such as: head seta P1 ventrad of A2, body with prominent L verrucae, elevated D and SD tubercles absent, D and SD setae closely appressed to the body, and prolegs very close together. Larvae of *C. leucomochla* differ from *C. aglaodesma* in having distinguishable primary SD setae, primary D setae surrounded by radiating secondary setae, and in lacking flattened scaliform secondary setae. The pupa of *C. leucomochla* is unknown.

Based on the illustration and description (Fletcher 1932), the larva of *C. pesseuta* is similar to those of *C. aglaodesma* and *C. leucomochla* in having prominent lateral verrucae bearing setae much longer than the D and SD setae. Differences include the presence of apically bifurcate setae and distinctly enlarged, exserted T1 and A8 spiracles in *C. pesseuta*. The pupa of *C. pesseuta* is similar to that of *C. aglaodesma* in having prominent adfrontal protuberances and lateral setae on verrucae. The pupa of *C. pesseuta* differs from *C. aglaodesma* in having longitudinal rows of secondary setae on the wings, dorsum with numerous minute to short secondary setae, and slightly exserted spiracles.

The genus *Cosmoclostis* has been placed in tribe Oxyptilini based on adult wing morphology, with the genera *Trichoptilus* Walsingham and *Megalorhipida* Amsel suggested as close relatives (Arenberger 1998, 2002). Gielis (2000, 2003) includes *Cosmoclostis* in the tribe Pterophorini based on his earlier revisionary study (1993) of the superfamily Pterophoroidea using adult characters. Characters of the larvae and pupae of *Cosmoclostis aglaodesma* support Gielis' tribal placement of the genus. In the larva, some of these characters include the presence of the adfrontal pore (AFa), labrum without a distinct notch and with setae M3 and L3 absent, and a 6-toothed mandible bearing only one seta. The adfrontal pore is present in Pterophorini and Oidaematophorini, as well as Agdistinae, Ochyroticinae, and 2 genera presently included in Platyptiliini. Pore AFa is lost in Oxyptilini, Exelastini, at least 13 genera of Platyptiliini, and Deuterocopinae (Matthews, unpublished data). A distinct labral notch, typically with a secondary median fissure is seen in the Oxyptilini, Exelastini, Platyptiliini, and Agdistinae, whereas a shallow rounded notch or a slight convex distal margin is present in tribes Pterophorini and Oidaematophorini. Six setae are present on the labrum of Pterophoridae except in the Pterophorini and Oidaematophorini where M3 and L3 are lost in the final instar. The pterophorid mandible usually has five teeth. A sixth tooth is present along the ventral margin in *Agdistis*, and in certain genera and species groups of Pterophorini and Oidaematophorini. A sixth tooth has not been found in Platyptiliini, Exelastini, or Oxyptilini. In the genus *Trichoptilus* (Oxyptilini) the mandible is reduced to 4 or 3 teeth, the smaller, most dorsal, tooth/teeth lost. The distal seta of the mandible is shorter than the proximal seta in most genera but it is extremely short or replaced by a pore in Pterophorini and Oidaematophorini. In *Agdistis*, 1 minute seta is found, with no second seta or pore evident.

Pupal characters supporting the placement of *Cosmoclostis* in tribe Pterophorini, as opposed to Oxyptilini, include the exposed coxa/trochanter of the fore leg, the mid legs not joined at meson, and the lateral setae of the abdomen arising from verrucae. Mosher (1916) first used the key character "Femora of the prothoracic legs exposed" vs. not exposed to distinguish between *Pterophorus* Geoffroy and *Oxyptilus* Zeller, based on *Hellinsia (Pterophorus) paleaceus* (Zeller) [Oidaematophorini] and *Geina (Oxyptilus) tenuidactylus* (Fitch) [Oxyptilini]. Examination of pupae containing pharate adults shows that this sclerite covers the coxa (anteriad) and trochanter (posteriad), and that the femur lies directly beneath the fore leg tibia. Yano (1963) correctly used the term coxa in his key to subfamilies, distinguishing Pterophorinae from Agdistinae and Platyptiliinae by "Coxa of fore leg exposed" vs. "Coxa of fore leg not exposed" respectively. We find this character to be very consistent, the fore leg coxa/trochanter sclerite is present in all examined genera of Oidaematophorini and Pterophorini and absent in the other pterophorid tribes.

The mesothoracic legs, specifically the mid leg tibiae of Ochyroticinae, Oidaematophorini and Pterophorini, (including *Cosmoclostis aglaodesma*), do not meet at any point along the meson. In Platyptiliini, Exelastini, Oxyptilini and Deuterocopinae, the midlegs are joined posteriad of the fore leg apex. In some species the mesothoracic legs are joined immediately posteriad of the fore leg but are distally parted where the maxilla tip is exposed. In Agdistinae, the maxilla may be thinly exposed along its entire length but the mid leg tips are joined posteriad of the maxilla apex.

Pupae with lateral setae on verrucae are found in certain genera and species groups of Oidaematophorini and Pterophorini, such as *Emmelina*, *Pterophorus*, *Oidaematophorus*, some *Adaina*, and some *Hellinsia*. Lateral tubercles may be present in other tribes or subfamilies but the primary setae are morphologically distinguishable from associated secondary setae on these tubercles. In the true verrucae of Oidaematophorini and Pterophorini, most of the secondary setae on the verrucae have distinguishable

"sockets" or are articulated, as are the primary D or SD setae.

While tribal placement of *Cosmoclostis* in Pterophorini can be supported, additional species need to be examined, to ascertain larval and pupal characters entirely unique to the genus *Cosmoclostis*. Continuing studies of larval and pupal structure will provide additional insight into the relationships between and within tribes and subfamilies of this group.

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Literature Cited

Arenberger, E. 1998. The types of the species of *Cosmoclostis* Meyrick (Lepidoptera: Pterophoridae) and their genitalia. Entomol. Scand. 28: 367-379.

Arenberger, E. 2002. Pterophoridae, 2. Teilband. *In*: Gaedike, R. (Ed) Microlepidoptera Palaearctica 11: 287 pp. Goecke & Evers, Keltern.

Fletcher, T.B. (Ed.). 1931. Catalogue of Indian Insects, part 20-Alucitidae (Pterophoridae). Government of India, Calcutta. 61 pp.

Fletcher, T.B. 1932. Life-histories of Indian Microlepidoptera. (Second Series) Alucitidae (Pterophoridae), Tortricina and Gelechiadae. Scientific Monograph No. 2. Imperial Council of Agricultural Research, Calcutta. 58 pp.

Fletcher, T.B. 1947. Some species of *Cosmoclostis* (Lep.: Alucitidae). Proc. R. Entomol. Soc. of Lond. (B) 16: 42-52.

Gielis, C. 1993. Generic revision of the superfamily Pterophoroidea (Lepidoptera). Zool. Verhand. Leiden 290: 1-139.

Gielis, C. 2000. Division of the Pterophoridae into tribes (Lepidoptera). Quadrifina 3: 57-60.

Gielis, C. 2003. Pterophoridae & Alucitoidea - *In*: World Catalogue of Insects 4: 1-198.

Heinrich, C. 1916. On the taxonomic value of some larval characters in the Lepidoptera. Proc. Entomol. Soc. Wash. 18: 154-164.

Hao, S.-L., Li, H.-H. , & Wu, C.-S. 2004. First record of the genus *Cosmoclostis* Meyrick from China, with descriptions of two new species (Lepidoptera, Pterophoridae). Acta Zoo. Sinica 29(1): 142-146.

Matthews, D.L. & Lott, T.A. 2005. Larval Hostplants of the Pterophoridae (Lepidoptera: Pterophoroidea). Mem. Amer. Entomol. Inst. 76: 1-324.

Meyrick, E. 1886. On the classification of the Pterophoridae. Trans. Entom. Soc. Lond. 1886: 1-21.

Mosher, E. 1916. A classification of the Lepidoptera based on characters of the pupa. Bull. Ill. State Lab. Nat. Hist. 12(2): 18-153, plates XIX-XXVII.

Nair, K.S.S. 2001. Pest Outbreak in Tropical Forest Plantations: Is There a Greater Risk for Exotic Tree Species? Center for International Forestry Research, Jakarta, Indonesia. 74pp.

Stehr, F.W. 1987. Order Lepidoptera. Pp. 288-596 *In* F.W. Stehr (ed.), Immature Insects [1], Kendall/Hunt, Dubuque. 754 pages.

Yano, K. 1963. Taxonomic and biological studies of Pterophoridae of Japan (Lepidoptera). Pac. Ins. 5(1): 65-209.

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ADDITIONAL RECORDS OF *CYCLARGUS AMMON* (LYCAENIDAE: LYCAENINAE) IN THE FLORIDA KEYS

Additional key words: *Caesalpinia*, colonization, Fabaceae, *Cyclargus thomasi bethunebakeri*, oviposition

Cyclargus ammon Lucas (Lycaenidae) is a small blue of the Bahamas, Cuba, and the Isle of Pines (Smith *et al.* 1994). Although historically reported from Florida, Calhoun *et al.* (2000) concluded with reasonable certainty that all such records actually represented those of the superficially similar *Cyclargus thomasi* Clench (Lycaenidae). In recent years, scattered anecdotal reports of *C. ammon* from south Florida continued to circulate but were not verified until 1997 and 1998 when several adults were photographed on Big Pine Key (Calhoun *et al.* 2000; Krizek 1998, 1999; Glassberg 1999). Since its initial discovery, regular additional sightings have persisted along with evidence of regular breeding colonies, indicating that the species has become firmly established. *C. ammon* has continued to increase in abundance and can now be found in many suitable habitat areas across Big Pine Key, but it has not been documented off the large island. We have found it to be locally common near patches of pineland *Acacia pinetorum* F. J. Herm. (Fabaceae) in open pine rockland habitat within the boundaries of Key Deer National Wildlife Refuge as well as along disturbed roadside areas on nearby private lands harboring sweet acacia, *Acacia farnesiana* (L.) Willd. (Fabaceae).

In June 2002, the U. S. Fish and Wildlife Service contracted the McGuire Center for Lepidoptera and Biodiversity to conduct a comprehensive one-year status monitoring survey of the now state-endangered Miami blue, *Cyclargus thomasi bethunebakeri* (Comstock & Huntington) (Lycaenidae) throughout its historic range and to gather detailed biological and ecological information on the remaining Bahia Honda State Park population. Concurrently, surveys were undertaken for the presence of *C. ammon* adults or active colonies on

FIG. 1. Female *Cyclargus ammon* collected in Bahia Honda State Park

the various islands surrounding Big Pine Key including Sugarloaf Key, Cujoe Key, Summerland Key, Ramrod Key, Big Torch Key, Middle Torch Key, Little Torch Key, No Name Key, West Summerland Key, Ohio Key, Missouri Key, and Little Duck Key. The survey did not include any of the backcountry islands. Despite ten visits between 19 July 2002 and 25 August 2003, no adults or immature stages were recorded. The resulting lack of sightings was not unexpected, owing to the species' close association with pine rockland forests, as only four of the islands (Little Pine Key, No Name Key, Sugarloaf Key and Cudjoe Key) support substantial remaining pockets of appropriate habitat.

Surprisingly, on 12 October 2002, a single adult female *C. ammon* was observed within Bahia Honda State Park. The individual was in relatively fresh condition and was encountered alongside *Leptotes cassius theonus* (Lucas) (Lycaenidae) and *C. thomasi bethunebakeri* on the far western portion of the island adjacent to a service drive at the base of a large artificial embankment. This embankment was originally constructed for the Henry Flagler East Coast Railway (now called the Old Bahia Honda Bridge). It is considered to be the primary visual landmark of the park and is a popular tourist attraction. Although this male was believed at the time to be merely an isolated vagrant, a second specimen, an adult female was encountered in the same general vicinity on March 21, 2003. The relatively fresh individual was captured and photographed (Fig 1) following several minutes of detailed observation during which it repeatedly oviposited on *Caesalpinia bonduc* (L.) Roxb. (Fabaceae).

This section of the island supports the largest remaining portion of the Miami blue population. It is comprised of beach dune and adjacent transition zone coastal strand with a resulting plant species composition that includes *Uniola paniculata* L. (Poaceae), *Ipomoea pes-camrae* (L.) R. Brown (Convolvulaceae), *Canavalia rosea* (Sw.) DC (Fabaceae), *Coccoloba uvifera* (L.) L. (Polygonaceae), *Lantana involucrata* L. (Verbenaceae), and *Pithecellobium keyense* Britt. ex Britt. & Rose (Fabaceae) along with several more typical hardwood hammock representatives such as *Heliotropium angiospermum* Murr. (Boraginaceae), *Conocarpus erectus* L. (Combretaceae), and *Metopium toxiferum* (L.) Krug & Urban (Anacardiaceae). The habitat was severely altered by the impact of Hurricane Georges on 25 September 1998, resulting in extensive disturbance and the introduction of *Caesalpinia bonduc*. This relatively aggressive, sprawling species, also known as gray nickerbean, now dominates much of the remaining community and serves as the only larval host for *C. thomasi bethunebackeri* on the island.

The two isolated sightings of *C. ammon* on Bahia Honda were clearly unexpected as the small state park does not harbor remnant tracts of pine rockland forest. Calhoun *et al.* (2000), in their description of the life history, list *Acacia pinetorum*, *Acacia farnesiana*, and *Caesalpinia pauciflora* (Griseb.) C. Wright ex Sauvalle (Fabaceae) as larval hosts utilized by the Big Pine Key population. To our knowledge, none of these plant species is known from Bahia Honda and they clearly do not occur on the western portion of the island where the two individuals were recorded. Although oviposition was observed on *Caesalpinia bonduc*, it is not known if this plant reliably serves as a viable larval host despite its suitability under laboratory conditions (Fine 2003). Nonetheless, the use of *Caesalpinia pauciflora* in Florida and the earlier record of *C. bahamenis* Lam. from Cuba (Alayo and Hernández 1987) suggest the likelihood that other members of the genus may also be utilized. If verified, it could influence the future range expansion of *C. ammon* throughout south Florida by enabling the colonization of many habitat areas previously unavailable due to a lack of suitable hosts. Additionally the use of *C. bonduc* would potentially place *C. ammon* in competition with *C. thomasi bethunebakeri* for available host resources at sites where the two species overlap.

While it seems unlikely that *C. ammon* has a regular presence on Bahia Honda, individual vagrants or even a small temporary breeding colony could easily be overlooked due to the species extremely close resemblance to *C. thomasi bethunebakeri*. Further research is needed on the ecological requirements and larval host range of *C. ammon* in south Florida, and its potential influence on the ongoing conservation efforts surrounding the endangered Miami blue.

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Literature Cited

Alayo, D., and L. R. Hernández. 1987. Atlas de las Mariposas Diurnas de Cuba (Lepidoptera: Rhopalocera). Edit. Cientifico-Tecnicia. Havana. 148pp.

Calhoun, J. V., J. R. Slotten, and M. H. Salvato. 2000. The rise and fall of tropical blues in Florida: *Cyclargus ammon* and *Cyclargus thomasi bethunebakeri* (Lepidoptera: Lycaenidae). Holarctic Lepid. 7(1): 13-20.

Fine, d. 2003. Variability of *Cyclargus ammon ammon*. So. Lep. News. 25 (3)

Glassberg, J. 1999. Nickerbean blues arrive in Florida. Amer. Butterflies. 7(2):22-23.

Krizek, G. O. 1998. *Hemiargus ammon* discovered in the USA at Big Pine Key, Florida (Lepidoptera: Lycaenidae). Holarctic Lepid. 5(2): 45.

________. 1999. Hemiargus *ammon* photographed in Florida. News Lepid. Soc.41:8.

Smith, D. S., L. D. Miller, and J. Y. Miller. 1994. The butterflies of the West Indies and South Florida. Oxford University Press. Oxford. 264 pp.

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NOTES ON THE OVIPOSITIONAL BEHAVIOR OF *LEPTOTES CASSIUS THEONUS* (LYCANIDAE: LYCAENINAE) IN THE LOWER FLORIDA KEYS

Additional key words: *Caesalpinia bonduc, Canavalia rosea, Dactyloctenium aegyptium,* polyphagous

Leptotes cassius theonus Lucas is a small, sexually dimorphic lycaenid found throughout Florida, the Bahamas, and the Greater Antilles (Smith et al. 1994). It is one of the most widely distributed butterflies in the Florida Keys, and frequents subtropical open to semi-open, sunlit habitats including beach dunes, coastal scrub, tropical pinelands, and tropical hardwood hammock margins, as well as urban gardens or parks (Minno and Emmel 1993). In many of these situations, the species seems to benefit from natural disturbance and anthropogenic activities that enhance the growth of pioneer vegetation or incorporate the introduction of ornamental plantings.

Within Florida, *L. cassius theonus* utilizes a variety of herbaceous and woody larval hosts in the Fabaceae and Plumbaginaceae; scattered representatives of the Malpighiaceae are also used by *L. cassius striatus* (Edwards) (Lycaenidae) in southern Texas. The developing larvae feed on the flowers and developing fruits of *Abrus precatorius* L., *Crotalaria incana* L. (Fabaceae), *Desmodium* Desv. (Fabaceae), *Lysiloma latisiliquum* (L.) Benth. (Fabaceae), *Galactia regularis* (L.) B.S.P. (Fabaceae), *Galactia striata* (Jacq.) Urban (Fabaceae), *Galactia volubilis* (L.) Britt. (Fabaceae), *Indigofera* L. (Fabaceae), *Macroptilium lathyroides* (L.) Urban (Fabaceae), *Phaseolus lunatus* L. (=*P. limensis*) (Fabaceae), *Piscidia piscipula* (L.) Sarg. (Fabaceae), *Pithecellobium keyense* Britt. ex Britt. & Rose (Fabaceae), *Pithecellobium unguis-cati* (L.) Benth. (Fabaceae), *Plumbago auriculata* Lam. (Plumbaginaceae), and *Plumbago scandens* L. (Plumbaginaceae) (Howe 1975, Minno and Emmel 1993, Scott 1986).

Detailed observations of the oviposition behavior of *L. cassius theonus* were conducted within Bahia Honda State Park in the Lower Florida Keys between July 2002 and August 2003. During much of the year, it is the most abundant blue encountered on the 524-acre island and regularly flies alongside *Hemiargus* (*Cyclargus*) *thomasi bethunebakeri* (Comstock & Huntington) (Lycaenidae) and *Hemiargus ceraunus antibubastus* Hübner (Lycaenidae) in many locations. In all but three instances, females exclusively elected to lay eggs on *Galactia volubilis* and *Pithecellobium keyense*. Both plants are common on the island, with *Galactia volubilis* being particularly prolific in open, disturbed sites alongside trails, service drives and roadways. Isolated oviposition events were documented on *Canavalia rosea* (Sw.) DC. (Fabaceae), *Caesalpinia bonduc* (L.) Roxb. (Fabaceae), and *Dactyloctenium aegyptium* (L.) Willd.(Poaceae) and represent new records for *L. cassius theonus*. In each case, a female landed on the plant, walked slowly over the vegetation while repeatedly probing it with her abdomen, and deposited a single egg before flying off. It is not known if *L. cassius theonus* larvae are able to successfully complete development on *C. rosea* or *C. bonduc*, although the likelihood of survival appears plausible due to the number of other similar fabaceous hosts utilized. By contrast, the choice of *D. aegyptium* clearly appears to

represent an oviposition error. The observation is particularly surprising owing to the fact that the grass was isolated in weedy picnic area several meters away from the nearest known viable host. Additionally, the female spent considerable time (~10 seconds) walking over the vegetation before depositing an egg.

The incidence of the unusual ovipositional behavior observed by *L. cassius theonus* may be explained by the fact that it utilizes over 15 different plant species in some 12 genera as larval hosts. Compared to more specialized species, which have been shown to make more rapid and/or accurate decisions regarding potential host acceptability, polyphagous species must properly recognize as well as rank a variety of available plant possibilities. As a result, individual decisions on whether to accept a plant as a viable host may take longer and/or lead to less accurate results (Bernays, 1988; Janz and Nylin, 1997; Nylin, 1988; Nylin et al., 2000).

LITERATURE CITED

BERNAYS, E. A. 1998. The value of being a resource specialist: behavioral support for a neural hypothesis. Amer. Nat. 151:451-464.
HOWE, W. H. 1975. The butterflies of North America. Doubleday & Co., Garden City, New York. 633 pp.
JANZ, N. AND S. NYLIN. 1997. The role of female search behavior in determining host plant range in plant feeding insects: a test of the information processing hypothesis. Proc. R. Soc. Biol. Sci. 264:701-707.
MINNO, M. C. AND T. C. EMMEL. 1993. Butterflies of the Florida Keys. Scientific Publishers, Gainesville, Florida. 168 pp.
NYLIN, S. 1988. Host plant specialization and seasonality in a polyphagous butterfly, *Polygonia c-album* (Nymphalidae). Oikos 53: 381-386.
NYLIN, S., A. BERGSTRÖM, AND N. JANZ. 2000. Butterfly host choice in the face of possible confusion. J. Insect Behav. 13 (4): 469-482.
SCOTT, J. A. 1986. The butterflies of North America. Stanford University Press, Stanford, California. 583 pp.
SMITH, D. S., L. D. MILLER, AND J. Y. MILLER. 1994. The butterflies of the West Indies and South Florida. Oxford University Press. Oxford. 264 pp.

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USE OF AN EXOTIC WEED AS AN OVIPOSITION SUBSTRATE OF THE HIGH-ANDEAN PIERID *PHULIA NYMPHULA*

Additional key words: Hirschfeldia, Brassicaceae, Argentina

The phenomenon of butterfly adaptation to exotic hosts is probably global. Shapiro (2002) and Graves and Shapiro (2003) documented the extensive use of exotic plants as oviposition substrates and larval hosts by native Californian butterflies. Most of the plants and thus most of the records are concentrated at low elevations. Shapiro (1991) gave numerous records of adaptation to exotic hosts for Pieridae in Argentina and suggested that use of weedy hosts may have facilitated the formation of hybrid zones in the genus *Tatochila* Butler. In a later paper (Shapiro 1997) he showed that such plants are being used by a significant proportion of the world's southernmost butterfly fauna, in extreme southern Patagonia and Tierra del Fuego. This paper reports the first case of this sort for the high-Andean fauna.

Phulia nymphula Blanchard (*sensu lato*; more than one genetic species is suspected to be involved) is the most widely-distributed of a lineage of mostly very small Pieridae endemic to the high Andes, the world's high-altitude Pierid record at about 5500m. *Phulia* and its close relatives are very small and display a variety of morphological and behavioral specializations, at least some of which reflect the pervasive importance of thermoregulation in their extreme environment. All the species of this lineage reared to date feed on Brassicaceae, such as the boreal genus *Draba*.

I first reported (Shapiro 1991) a new southern limit for *P. nymphula* in the Andes, in the vicinity of the Las Lenas ski resort in southwestern Mendoza province, Argentina, based on collections and observations made in the austral spring of 1989. At that time the butterfly was seen only at or above 3000m. No host plant was identified. I revisited the area in the austral summer of 2004. During the intervening 15 years the Mediterranean Brassicaceous weed *Hirschfeldia incana* (L.)Lagr.-Fossat (usually referred to in the literature as *Brassica geniculata* (Desf.)Ball) became established around the ski village complex at about 2250m. On 2 February 2004 *P. nymphula* was abundant throughout the complex. Adults visited flowers of *H. incana* and eggs were being laid on small rosettes (diameter under 6 cm). No other Brassicaceous plants were observed in the area. I did not look for larvae, being pressed for time. Strikingly, females showed no interest in ovipositing on the large plants. Numerous courtships and pairs in copula were noted.

Hirschfeldia is not a very common weed in western Argentina. In California it is a very frequent host of

weedy Pieridae including *Pieris rapae* L. and *Pontia protodice* Bdv. & LeC., but it is almost never seen above 1500m and is completely absent in climates comparable to that at Las Lenas. The erect, even bushy growth form of this plant has no analogue in the native brassicaceous flora of the high Andes. It would seem *P. nymphula* has successfully colonized this plant by focusing strictly on small rosettes, whose growth form, with tightly imbricated leaves, is familiar to it as the mature plant is not.

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LITERATURE CITED

GRAVES, S.D. & A. M. SHAPIRO. 2003. Exotics as host plants of the California butterfly fauna. Biol. Cons. 110: 413-433.

SHAPIRO,A. M. 1991. The zoogeography and systematics of the Argentine Andean and Patagonian Pierid fauna. J.Res.Lepid. 28:137-238.

—— 1997. Impactos antropogenicos sobre la fauna de mariposas (Lepidoptera: Rhopalocera) de Patagonia austral y Tierra del Fuego. Anales Instituto de la Patagonia (Punta Arenas, Chile), Ser.Cs.Nat. 25: 117-126.

—— 2002. The Californian urban butterfly fauna is dependent on alien plants. Diversity & Distributions 8: 31-40.

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SURVIVAL OF FREEZING AND SUBSEQUENT SUMMER ECLOSION BY THREE MIGRATORY MOTHS: *MANDUCA SEXTA* AND *HYLES LINEATA* (SPHINGIDAE), AND *HELICOVERPA ZEA* (NOCTUIDAE).

Additional key words: overwintering, *Heliothis virescens*

Hyles lineata (Fabricius) and *Helicoverpa zea* (Boddie) are well known migrants whose overwintering limits are apparently poorly known. Winter pupal diapause has been previously discussed (e.g. Johnson, 1995) for *H. zea* in Arkansas, and for other *Helicoverpa* species on other continents (e.g. Gregg *et al.*, 1995). However, while Ferguson (1991) listed *Manduca sexta* (Linnaeus) as a migrant, McNeil *et al.* (1995) repeatedly referred to it as non-migratory. All three species range into the Neotropics. Most southern migrants listed by Ferguson peak in September, October or November in southern New Jersey, but *M. sexta* does not. The latest specimen date found for *M. sexta* for New Jersey, Pennsylvania, or Delaware (collections of Rutgers University, University of Delaware, W.J. Cromartie, the late Joseph Muller, myself) is 12 September and 87% of 30 available specimen and observation dates are from 6 July to 4 September, which includes a partial second brood (my rearings in Connecticut and New Jersey). Jones (1928–1929) reports mid July through August for Delaware, and Smith (1910) and Tietz (1952) report none after September for New Jersey and Pennsylvania. Pupal diapause increases from about 5% in June to 95% in mid August even in northern Florida (Villanueva, 2005). Furthermore, although the related migrants *Agrius cingulatus* (Fabricius) and *M. quinquemaculata* (Haworth) have both been collected several times far to the north in Maine (Brower, 1974), Vermont (Grehan *et al.*, 1995), Nova Scotia (Ferguson, 1955), and Quebec (Handfield, 1999) often in September and October, the generally more common *M. sexta* is unreported by any of those sources. All of these factors suggest northeastern populations of *M. sexta* are not strongly migratory, but occurrence on Bermuda and in the Galapagos Islands (Ferguson, 1991) seems to affirm migratory status elsewhere.

In late November 2001 I unexpectedly found a still living pupae of *Helicoverpa zea* from a caterpillar reared from local (Cumberland County) corn in late summer in a small plastic container with a few cm of peat. I placed it indoors for two weeks and when it did not develop, I moistened the peat, put it in my refrigerator, and returned it to ambient conditions on 15 March. In late November 2002, four small peat-filled containers each containing an *H. zea* pupa from larvae on local corn or bell pepper were packed among dead leaves inside a large Styrofoam box with numerous other pupal containers. I placed the box in a coal bin off my house, which is mostly enclosed, but outside, unheated, and with a floor of natural ground. Three other *H. zea* that had entered the soil as prepupae 30 August to 9 September 2002 eclosed later that month, providing strong evidence that these four, which were also prepupal on or before 10 September, were in diapause. All larvae were reared outdoors.

In October 2002 Robert Barber gave me three small

black form *Hyles lineata* larvae he collected on large, weedy, *Rumex* at Port Norris, New Jersey, where I reared them outdoors on the same hostplant. The first made a pupal cell among paper towel on 22 October and another about a week later. Both pupated in November and were placed in a small, ventilated plastic container also in the Styrofoam box. In late October 2002, Thomas Mullane gave me a *Manduca* pupa he dug from his tomato patch in nearby Cedarville. I left it outside in a ventilated plastic container with no insulation until early December (about -3° to 20°C) before packing it in moist peat and placing it with the *Helicoverpa* and *Hyles*. The winter of 2002–2003 was the coldest in more than fifteen years and the air temperature in the coal bin was below freezing for about half of January and February and twice fell to -5.5° C. Ice crystals were observed in the peat containing these pupae. All containers were returned to shaded ambient conditions in mid March.

An *H. zea* eclosed on 29 June 2002 from the larva prepupal 9 September 2001, and two on 8 and 12 July 2003 from larvae prepupal 10 September 2002. Two pupae died at unknown times. Both *H. lineata* pupae were alive on 1 June 2003 and one produced tachinids later that month and the other a female moth 9 July. A wild adult was seen 25 June that year. A male *M. sexta* eclosed at dusk on 7 July 2003. Despite the small sample sizes, these observations directly demonstrate that overwintering pupae of *M. sexta*, *H. lineata*, and *H. zea* can tolerate slightly sub-freezing temperatures sufficient to freeze their immediate substrate, although *H. zea* and *M. sexta* in insulating icy peat certainly were not exposed to -5.5°C. Furthermore Jeff Fengler (pers. comm., 31 January 2004) reports digging up a pupa in early spring at Shelton, Connecticut (41.3° North), which produced an adult *M. sexta*, directly documenting survival where winters average well below freezing about 250 km west-southwest of the species' range limit near Boston, Massachusetts (42.5°North).

Since pupae can survive slightly subfreezing temperature, *H. zea* should be able to overwinter farther north than southern Arkansas (33.2° North) as reported by Johnson (1995), although no southern migrants he discusses appear to overwinter successfully to the 0°C January isotherm. I collected a worn runty female with malformed wings and impaired flight at Millville, New Jersey (39.4° North, January mean +0.6°C) flying diurnally on 13 July 1994 that virtually had to come from a locally overwintered pupa. Since I am aware of only one record before 9 June for New Jersey (Rutgers collection, 28 May 1974) and none before 15 June from similar latitudes in Delaware (Jones, 1928-1929, Univeristy of Delaware collection) or Ohio (Rings *et al.*, 1992), local eggs by early June would be extremely unlikely, and with cooler conditions and probably suboptimal food, development of this moth from oviposition to eclosion in early July would have required longer than the 35 to 44 days required under optimal conditions (Stewart, 2003, Hardwick, 1996). Observations from Arkansas (Johnson, 1995) suggest the earliest adults (often late June in New Jersey) would probably be migrants and since my eclosion dates were 29 June to 12 July it is quite likely July–early August adults include some from locally overwintered pupae.

Perhaps the most interesting observation is that adults of all three species eclosed in summer, despite the fact that they start in early spring or fly nearly all year much farther south (e.g. Hardwick, 1996, Vallanueva, 2005) and that non-diapausing pupae of *H. zea* hatch in about two weeks and *M. sexta* in about three weeks in late summer. The heat requirements to terminate diapause and complete subsequent development for both species appear similar to resident heliothine Noctuidae and many Sphingidae which eclose in June or later in southern New Jersey. Therefore a lack or scarcity of spring adults northward is not valid evidence that pupae of multivoltine migratory moths perish over winter northward, as lepidopterists often assume.

Since overwintering pupae of these three species can survive slightly subfreezing conditions, they probably could survive in moderately cold climates. Furthermore *Manduca sexta* pupae at 10–15 cm deep (Villanueva, 2005) would experience only a few degrees below freezing even at their range limit in southern New England, where I report an instance of overwintering in the field, and would remain above freezing in many southern New Jersey winters. Although the evidence suggests some local overwintering, *Helicoverpa zea* is obviously reinforced by immigrants from the south in New Jersey, as is well documented for much of North America, and may even have some southward return in fall (Johnson, 1995). However, *M. sexta* populations in the northeastern USA probably do not depend on immigrants. Freeze tolerance, diapause, and the brief mid-summer peak flight season seem well adapted to the climate at the northeastern limit of the range. *Hyles lineata* is currently uncommon enough in New Jersey that its status is unclear and the species is essentially absent now farther to the northeast. Finally I note obtaining one eclosion, in late May, after overwintering three local autumn pupae of another heliothine pest migrant, *Helitothis virescens* (Fabricius), in my refrigerator.

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Literature Cited

Brower, A.E. 1974. A List of the Lepidoptera of Maine-Part 1 the Macrolepidoptera. Life Sci. and Agric. Expt. Sta., Univ. of Maine at Orono. 136 pp.

Ferguson, D. C., 1955. The Lepidoptera of Nova Scotia part 1 Macrolepidoptera. Bull. no. 2 Nova Scotia Museum of Science, Halifax, NS. 375 pp.

Ferguson, D. C. 1991. An essay on the long-range dispersal and biogeography of Lepidoptera, with special reference to the Lepidoptera of Bermuda. Mem. Entom. Soc. Canada 158: 67–84.

Gregg, P. C., G.P. Fitt, M. P. Zaluki, and D.A.H. Murray. 1995 Insect migration in an arid continent . II. *Helicoverpa* spp. in eastern Australia, pp. 151–172. *In* Drake, V. A. and A. G. Gatehouse (eds). Insect Migration: tracking resources through space and time. Cambridge Univ. Press, Cambridge, England; New York, NY, USA; Melbourne, Australia. 478 pp.

Grehan, J. R., B. L. Parker, G. R. Nielsen, D. L. Miller, James D. Hedbor, M. Sabourin, and M. S. Griggs, , 1995. Moths and Butterflies of Vermont (Lepidoptera), a faunal checklist. Agric. Expt. Sta., University of Vermont; Vermont Dept. of Forests, Parks, and Recreation, misc. publ. 116; Vermont Monitoring Coop. Bull. no.1., 94 pp., 4 plates.

Handfield, Louis. 1999. Le Guide des Papillons du Quebec. Version Scientifique. Broquet, Boucherville, Qc., Canada 982 pp., + 123 color plates.

Hardwick, David F. 1996. A Monograph of the North American Heliothentinae (Lepidoptera: Nocvtuidae). Centre for Land and Biological Resources Research, Agriculture Canada, Ottawa. 255 pp.

Jones, Frank Morton. 1928–1929. Lepidoptera of Delaware, peninsular Maryland and Virginia. Unpublished ms., Claude E. Phillips Herbarium, Delaware State Univ., Dover.

Johnson, S. J., 1995. Insect migration in North America: synoptic-scale transport in a highly seasonal environment, pp. 31–66. *In* Drake, V. A. and A. G. Gatehouse (eds.), Insect Migration: tracking resources through space and time. Cambridge Univ. Press, Cambridge, England; New York, NY, USA; Melbourne, Australia. 478 pp.

McNeil, J. N, M. Cusson, J. Delisle, I. Orchard, and S.S. Tobe. 1995. Physiological integration of migration in insects, pp. 265–277 *In* Drake, V. A. and A. G. Gatehouse, Insect Migration: tracking resources through space and time. Cambridge Univ. Press, Cambridge, England; New York, NY, USA; Melbourne, Australia. 478 pp.

Rings, R. W., E. H. Metzler, F. Jarrod, and D.H. Harris. 1992. The Owlet Moths of Ohio. Bull. Ohio Biological Survey, new series, vol. 9 (2), Ohio State University, Columbus, OH. 187 pp., 16 plates.

Smith, J.B. 1910. The Insects of New Jersey. Annual Report of the New Jersey State Museum for 1909, Trenton, NJ, 888 pp.

Stewart, Scott D. 2003. Cotton insects: bollworm. Agricultural Extension Service. University of Tennessee, website, visited January 2005 and 2 February 2006. http://www.utextension.utk.edu/fieldCrops/cotton/cotton_insects/Pests/bollworm.htm

Tietz, Harrison M., 1952. The Lepidoptera of Pennsylvania. Pennsylvania State University, School of Agriculture, State College, Pennsylvania. 180 pp.

Villanueva, Raul, 2005. Featured creatures: tobacco hornworm, *Manduca sexta* (Linnaeus). University of Florida Institute of Food and Agriculture Sciences, Dept. of Entomology and Nematology and Florida Dept. of Agriculture and Consumer Services website, visited January 2005 and 2 February 2006. http://creatures.ifas.ufl.edu/field/hornworm.htm.

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NOTES ON ASPECTS OF THE LIFE HISTORY AND BEHAVIOR OF *COLEOTECHNITES ERYNGIELLA* (GELECHIIDAE).

Additional key words: *Eryngium*, herbivory, tallgrass prairie, Illinois

The Gelechiidae is one of the largest families of microlepidoptera, with between 4,300–4,600 species estimated worldwide (Hodges 1998, Arnett 2000); 87 genera and 813 species have been recorded from the U.S. and Canada (Arnett 2000). This number may be an understatement as only 30% of the Nearctic species have been described (Hodges 1998). In North America, there are approximately 47–49 species of *Coleotechnites*, of which eight are considered pest species, mostly on coniferous trees and shrubs. These pest species damage plants by eating the foliage and mining through the leaves/needles (Arnett 2000, Mississippi Entomological Museum 2005). Although numerous studies have been done on the pest species in this genus, very few, if any, studies have examined *Coleotechnites eryngiella* (Bottimer, 1926).

It is important to note that members of the family Apiaceae have a broad chemical diversity, and that the presence of secondary compounds mediates plant-animal interactions. As a result very few insects are capable of feeding on the plant parts of members of Apiaceae, and those insects that are capable of feeding on members of this family are often highly specialized (Berenbaum 2001). Currently only two species of Lepidoptera are recorded as having larvae that feed on the plant parts of *E. yuccifolium*: *C. eryngiella* (Molano-Flores 2001 [moths were originally misidentified as *Aristotelia* sp., but were later determined to be *C. eryngiella* by Terry Harrison], pers. obs.) and *Papaipema eryngii* Bird, 1917 (Noctuidae), an Illinois state-threatened species whose larvae bore into the inflorescence stalks (Panzer and Derkovitz 1992). Here I provide some information regarding the life history and behavior of *C. eryngiella* as well as suggestions for

future research.

Description of *Coleotechnites eryngiella*. *C. eryngiella* was originally described by Bottimer (1926) as a species of the genus *Recurvaria*. This species is a small moth (approx. 6 mm in length, 15 mm wingspan) that closely resembles *Coleotechnites variella* (Chambers, 1872) and *Coleotechnites apicitripunctella* (Clemens, 1860). According to Bottimer (1926), *C. eryngiella* differs from *C. variella* in that it has labial palpi and legs marked with black, and it differs from *C. apicitripunctella* in that its face, head and thorax are white and it lacks annulations on its antennae (Fig. 1). The larvae of this species are pink and white-striped (Fig. 1) and have been reported to feed on two species of *Eryngium* (Apiaceae): *Eryngium yuccifolium* (Molano-Flores 2001, pers. obs.) and *Eryngium aquaticum* (Bottimer 1926). The report of *C. eryngiella* on *E. aquaticum* is likely incorrect because the range of *E. aquaticum* does not extend into Texas where Bottimer originally collected the specimen and because the name *E. aquaticum* has been misapplied to plants of *E. yuccifolium* (Mathias and Constance 1941, Gleason and Cronquist 1991).

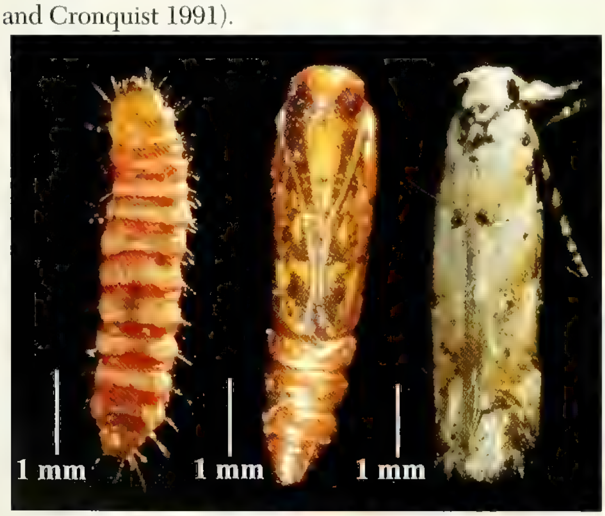

FIG. 1. The larval, pupal and adult stages of *Coleotechnites eryngiella*.

Observations and Collection Records. During a study examining the effect of herbivory on the reproductive biology of *E. yuccifolium* (Danderson 2005), live larvae and pupae (Fig. 1) were found in inflorescence heads collected from five tallgrass prairie sites: Grant Creek Prairie (Will Co.), Loda Cemetery Prairie (Iroquois Co.), Pellville Cemetery Prairie (Vermilion Co.), Prospect Cemetery Prairie (Ford Co.) and Weston Cemetery Prairie (McLean Co.), in Illinois between late August and early October in both 2003 and 2004. The majority of central and primary lateral inflorescence heads contained between one and seven larvae. The inflorescence heads that were collected were placed within 2 $\frac{1}{4}$" x 3 $\frac{1}{2}$" manila envelopes which were then placed in plastic sandwich bags and stored at indoor room temperature (20 °C). Within two or three weeks, silky cocoon-like structures containing larvae or pupae could be seen inside the plastic bags. When envelopes were opened in November and December to access the inflorescence heads for dissection, silky cocoon-like structures with empty pupal cases and dead adult moths were often present in the envelope. Storing the inflorescence heads at room temperature likely hastened the transition from larvae to adult.

In *E. yuccifolium*, the larvae feed by boring tunnels into the ovaries and developing mericarps of the flowers (Fig. 2). These tunnels are often lined with silk and full of frass, and shed head capsules from the larvae are common as they change instars. The damage is often extensive, with more than 70% of the flowers showing signs of herbivory (Danderson 2005). Damaged inflorescence heads can be easily differentiated by dark, brown patches of damaged flowers.

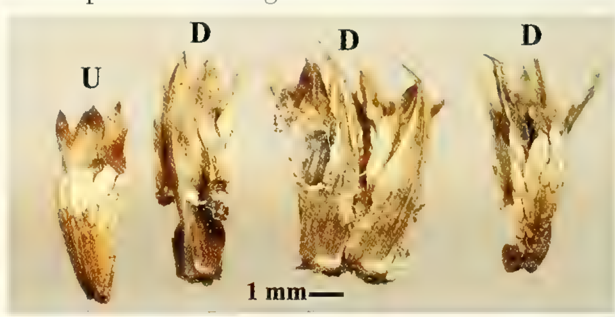

FIG. 2. Undamaged mericarps of *Eryngium yuccifolium* (U) alongside mericarps damaged by the larvae of *Coleotechnites eryngiella* (D).

The populations of *C. eryngiella*, in terms of larvae collected from the inflorescence heads, seemed to vary within sites among years. Grant Creek in 2003 experienced a drastic reduction in the local population of *C. eryngiella* following an accidental prairie burn that burned a large proportion of the prairie. For example, 55% of the mericarps in the central inflorescence heads showed signs of herbivory at Grant Creek in 2000. Following the accidental burn in 2003, 0% of the mericarps in the central inflorescence heads showed signs of herbivory. The Loda site in 2004 experienced a similar, yet not as drastic, population reduction as a result of a prescribed burn on half of the site. In this instance, 37% of the mericarps in the central inflorescence heads showed signs of herbivory in 2003 compared to 10% of the mericarps in the central inflorescence heads in 2004 (Danderson 2005).

During the winter of 2004, I visited the Loda, Pellville and Prospect sites and collected 20 inflorescence stalks at both Loda and Prospect and 10

inflorescence stalks at Pellville. The inflorescence stalks and heads were then dissected and examined for the presence of *C. eryngiella*. Examination of the stalks and inflorescence heads showed no evidence of *C. eryngiella* over-wintering on *E. yuccifolium*; however, among the mericarps and persistent bracts of the inflorescence heads I did find empty pupal cases and dead larvae. Unlike the flowers in the inflorescence heads, there was no evidence that *C. eryngiella* damaged the receptacles of the inflorescence heads or the inflorescence stalks.

During the late spring and summer of 2004, a study examining the effects of herbivory and inflorescence size on pollinator/visitor attraction for *E. yuccifolium* was conducted (Danderson 2005). For this study, the inflorescences of 30 plants that showed no signs of herbivory were covered by fine mesh netting between May 30 and June 22 at Grant Creek, Loda, Pellville, Prospect and Weston. By early July, some of the netted plants showed signs of herbivory. When the inflorescence heads were opened, *C. eryngiella* larvae were present. Similar observations were made by Molano-Flores (2001) when she covered inflorescences with netting in late June for her 1998 study on the reproductive biology of *E. yuccifolium*.

Although no adults were collected by UV light for this study, adults of this species have been collected in prairies and forest in other states by UV light, primarily in the southern US. Collection information for these specimens provides an insight to when adults of this species are present. Most of the specimens held at the Mississippi Entomological Museum (MEM) in Mississippi State, MS were collected by UV light from a few locations in Alabama, Mississippi and Louisiana. The specimens from Alabama were collected from forest habitat in late June and early August. The specimens from Louisiana were collected from forest habitat in late May, early June, early August and mid-September. Specimens from Mississippi were collected in early April, late May, early June, late July and late August in prairie habitat and in late May in forest habitat.

Interpretations of Observations and Collection Records. From the observations and collection records, some aspects of the life history of *C. eryngiella* have become clarified while other aspects remain speculative. It is unclear whether this species is univoltine, bivoltine, or multivoltine in Illinois. Adults have been collected as early as April and as late as September in the southern US and from these collection records this species appears to be bivoltine or possibly multivoltine in the South. However, numerous collections within sites at regular intervals from spring to fall are needed for confirmation. Also, voltinism patterns may vary across its range.

Eggs may be laid in the developing inflorescences of *E. yuccifolium* early in the spring, possibly between April and May (Molano-Flores 2001, Danderson 2005), as suggested by the lack of empty egg cases on the foliage or on the inflorescence stalks in late spring. If this species is bivoltine or multivoltine, eggs may be laid in the inflorescence heads later in the summer as well.

Evidence suggests that this species likely diapauses as pupae; larvae are readily collected in late summer and early fall, eggs are laid in spring, and larvae and eggs are absent in the persistent inflorescence stalks and receptacles. There was no evidence to suggest that *C. eryngiella* over-winters in the persistent inflorescence stalks; however, this species might over-winter in the dispersed mericarps. In autumn, the mericarps tend to fall off the receptacle of the inflorescence, and, in view of the fact that pupae and silky cocoon-like structures have been observed in the tunneled-out mericarps from inflorescences collected during fall, diapause inside the mericarps seems likely. Diapause in mericarps amongst the leaf litter at the base of the plants may explain why populations of this moth tend to experience a decline in the season following a prescribed burn (i.e., Grant Creek in 2003 and Loda in 2004, pers. obs.).

C. eryngiella may have a large range. Collections of larvae and adults of this species have been made in Alabama, Illinois, Louisiana, Mississippi and Texas (Bottimer 1926, Mississippi Entomological Museum 2005, pers. obs.). However, like many microlepidoptera species, this species has been under-collected and as a result, the full extent of its range is poorly understood. Potentially, the range of this species could correspond with the range of *E. yuccifolium*, which extends from Connecticut west to Minnesota and south from Florida to Texas (Mathias and Constance 1941, USDA 2004). Also, it is not known whether this moth feeds on the other 18 species of *Eryngium* east of the Rocky Mountains or other unrelated taxa, but if it does then the range of *C. eryngiella* could be even larger.

Many aspects of the life history of this moth and its relationship with *E. yuccifolium* and prairie habitat have yet to be studied. Much is speculative and needs further clarification. Previous studies (Molano-Flores 2001, Danderson 2005) have only examined the effect of *C. eryngiella* on the reproductive biology of *E. yuccifolium* and have demonstrated that the presence of this moth can greatly reduce the number of seeds produced, directly by damaging the seeds or indirectly by causing floral damage that limits an individual plant's ability to attract pollinators. For example, at Grant Creek in 2003 when 0% of the mericarps in the central inflorescence heads showed signs of herbivory due to

the accidental burn, the central inflorescence heads had a mean seed set of 62%. By comparison, 72% of the mericarps in the central inflorescence heads showed signs of herbivory and the central inflorescence heads had a mean seed set of 13% at Grant Creek in 2004 (Danderson 2005). Currently, only one long-term study is examining the effect that *C. eryngiella* may have on populations of *E. yuccifolium* in remnant and restoration prairies (Molano-Flores pers. com.). The effects of prescribed burns on *C. eryngiella* are relatively unknown, although preliminary evidence suggests that their populations can be drastically reduced following a prescribed burn. Studies examining the long-term effects of prescribed burns on the relationship between *C. eryngiella* and *E. yuccifolium* are also suggested.

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LITERATURE CITED

ARNETT, JR., R. H. 2000. American insects: a handbook of the insects of America North of Mexico. 2nd edition. CRC Press, New York, NY. xx + 1003 pp.

BERENBAUM, M. R. 2001. Chemical mediation of coevolution: phylogenetic evidence for Apiaceae and associates. Ann. Missouri Bot. Gard. 88: 45-59.

BOTTIMER, L. J. 1926. Notes on some Lepidoptera from Eastern Texas. J. Agric. Res. 33: 797-820.

DANDERSON, C. A. 2005. The effects of herbivory by a moth (Gelechiidae: *Coleotechnites eryngiella* Bottimer) on rattlesnake-master (Apiaceae: *Eryngium yuccifolium* Michaux). M.S. Thesis, Department of Plant Biology, University of Illinois, Urbana, Illinois. vii + 128 pp.

GLEASON, H. A. & A. CRONQUIST. 1991. Manual of vascular plants of northeastern United States and adjacent Canada. 2nd edition. The New York Botanical Garden Press, Bronx, NY. xlvi + 994 pp.

HODGES, R. W. 1998. Gelechioidea, pp. 130-158. *In* Kristensen, N.P. (ed.), Lepidoptera, moths and butterflies. Handbook of zoology/Handbuch der zoologie 1(1999). Berlin and New York.

MATHIAS, M. E. & L. CONSTANCE. 1941. A synopsis of the North American species of *Eryngium*. Amer. Mid. Nat. 25: 361-387.

Mississippi Entomological Museum, Mississippi State University. 2005. Global Framework of Gelechiidae.(http://www.msstate.edu/org/mississippientmuseum/Researchtaxapages/Gelechiidae-home.html). Mississippi State University, Mississippi State, MS. (Accessed: March 14, 2005).

MOLANO-FLORES, B. 2001. Reproductive biology of *Eryngium yuccifolium* (Apiaceae), a prairie species. J. Torrey Bot. Soc. 128: 1-6.

PANZER, R. & G. DERKOVITZ. 1992. A survey of butterflies and *Papaipema* moths of Grant Creek Prairie Nature Preserve, Will County, IL. A study completed for the Illinois Department of Conservation, Springfield, IL.

USDA, NRCS. 2004. The PLANTS Database, Version 3.5 (http://plants.usda.gov). National Plant Data Center, Baton Rouge, LA 70874-4490 USA. (Accessed: March 14, 2005).

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REMEMBERING DON MACNEILL

At the 2005 Annual Meeting of the Lepidopterists' Society, held shortly after Don's death, the authors agreed to contribute personal remembrances of Don MacNeill, as a supplement to a more traditional biographical obituary (immediately following these remarks) outlining his contributions to California natural history and the study of Lepidoptera. We solicited contributions from others, with the hope that the resulting article would allow the readership of our society to know something of this generous, knowledgeable, and entertaining lepidopterist and friend. We have not unduly deleted overlap or duplication of experience, both to avoid diluting each contributor's remembrance, and as a means to accent aspects of Don's personality, such as the enjoyment he obviously derived from introducing friends, new to California, to the eastern slopes of the Sierra Nevada.

Charles Don MacNeill
1924-2005

Don MacNeill, an outstanding ecologist, noted hesperiid specialist, patient mentor, and really fine person, died of heart failure on July 28, 2005, at the age of 80. His extensive knowledge, thoughtful reasoning, and friendly nature will be missed by all of us who knew him.

Don was born in San Francisco—a several generation native Californian—and raised in Oakland. As a young boy his interest and dedication to biology was encouraged by Mel Johansen, who was the exhibits preparator at the Snow Museum, a quaint predecessor of the Oakland Museum, where MacNeill eventually spent most of his career. Don's passion was further fostered by Milford Lundgren, his junior high school biology teacher and ultimately long time friend and collaborating insect collector.

After one semester at the University of California, Davis, Don was drafted into World War II and served in the Air Corps as a radio operator and mechanic with a tow-target squadron, mostly in Hawaii. In March 1945 he married his high school girlfriend, Grace, and after discharge at the end of the war he returned to Davis to major in zoology and wildlife management. However, inspired by a basic course in entomology taught by R. M. Bohart, Don's emphasis abruptly shifted to insects; and he transferred to Berkeley, where the program was more varied (the Department of Entomology was shared by both campuses at that time). He completed a B.S. degree in 1950 and continued in the systematics program in graduate school at Berkeley, under the direction of E. G. Linsley. His thesis involved a biological and taxonomic study of skippers of the genus *Hesperia* in western North America. In addition to field work in the southwestern U.S., Don spent three months in 1952 traveling extensively in Mexico, accompanied by E. E. Gilbert; they collected insects in amber, the type series of *H. uncas gilberti*, and a great many other insects.

Twin daughters, Nora and Daren, were born in 1953 and daughter Linn in 1956. In 1957 MacNeill took a position as assistant curator at the California Academy of Sciences in San Francisco and continued his thesis research and writing at home evenings, filing the dissertation in 1960. Throughout his tenure in graduate school, at the Academy, and later in his professional career, he served as a mentor to many others. He was

always generous with his time, sharing his knowledge and helping students pursue their interests in natural history. It is tempting to wonder if he missed his calling by not having filled an academic position, but he seemed to excel in a one-on-one role.

Unfortunately for Lepidoptera research but fortunately for a broad audience in natural history, the position at the Academy lacked permanency. So when plans for the new Oakland Museum included hiring curators to develop new concepts in exhibits and public education, Don accepted a position as Associate Curator in 1965, acting as an advisor and planner of the natural history exhibits. Later he became Senior Curator and director of research and planning—the conceptual architect of the museum's California ecology gallery. Rather than the traditional approach, showing large mammals and birds in an African or other exotic diorama, or exhibit cases with rows of butterflies, MacNeill perceived a transect of habitats across California, from seacoast and chaparral foothills through inland valleys and the high Sierra Nevada to the arid Great Basin east of the Sierra. His research and development spanned more than a decade, gradually expanding the exhibits long after the museum was open to the public. Each depicts the ecological relationships of varied organisms—plants, insects, herps, birds, mammals—and their interrelated roles. The exhibits in total form a naturalist's walk across California. Each is based on real places and dynamic events, for example, a decaying log and its inhabitants, the fire-based maintenance of a chaparral habitat, and an alpine lake near Mono Pass at 12,000 ft., the "luncheon meadow" where many of us were coaxed to accompany him during the search for *Hesperia miriamae*. First time visitors to the museum are perhaps puzzled by the lack of names and numbers for the organisms, but the overall effect is innovative, long-lasting, and worth revisiting many times.

Beyond his responsibilities at the Oakland museum, Don worked nights and weekends to complete a monographic treatment of Nearctic Hesperiidae, for which he is perhaps best known, published in *The Butterflies of North America*, edited by W. H. Howe. He made several trips to Mexico (Durango-Sinaloa, Nayarit, Jalisco, Coahuila, Nuevo Leon) and the Dominican Republic in search of skippers during the subsequent 20 years, and was a research fellow at the Australian National Collection, C.S.I.R.O., to conduct research on the biology of trapezetine Hesperiidae in 1981. He also was a published fern expert and made trips with Alan Smith in search of rare, ones, many of which he cultivated. After retirement in 1989, MacNeill continued his research on skippers, especially *Polites* and *Hylephila*, and carried out field work in the southwestern U.S. and Chile. He used the California Academy as a base, renewing a long term attachment to the CAS collection, usually working there three days a week, despite an increasingly congested commute, until a few weeks before his death. His extensive private collection of Hesperiidae has been given to the CAS.

Don MacNeill joined The Lepidopterists' Society in the 1950s, presented a talk on behavior of hesperiids at the first annual meeting of the Pacific Slope Section in 1954, another in 1959 in Santa Barbara, and hosted the 7th Pacific Slope annual meeting at the CAS in 1960 and the 19th at Oakland Museum in 1972. He was a member-at-large of the Executive Council 1966-1969. Don was a member of many ecological and entomological societies and president of The Pacific Coast Entomological Society in 1966, as well as member and a director of advisory boards for various agencies dealing with land resources, the UC Botanical Garden, and so on. But he was not comfortable in large group situations, especially as a speaker, and rarely attended society meetings in his later years—and then only as an adjunct to field work. He attended a few during retirement, as recently as the Pacific Slope meeting in 2002.

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I met Don MacNeill in 1961 at the California Academy of Sciences where I had been hired as a temporary employee. My job was to transfer beetles from wooden boxes to the academy drawers. I found the pull of butterflies to be much greater than that of the beetles. So, I spent as much time with Don as I could. We formed a friendship that lasted forty-three years. When weather permitted we would spend our lunch time visiting the San Bruno Mountains, Twin Peaks, or some other interesting place. Don was always willing to be helpful in answering my questions. His willingness went as far as letting me car pool to work from his home. During those trips we had many discussions of butterflies, future collecting trips, and how we would solve the problems of the world. During this time I met his wife Grace, and his three daughters, as well as admiring his collection and laboratory that sat over the garage.

I will always remember the good times we had on the trips to the Mojave Desert and the long hikes to Mono Pass for *Hesperia miriamae*. It was during one of these trips that I met Don's junior high school teacher and long time friend Milford Lundgren.

When Don moved to the Oakland Museum in 1965, I lost contact with him and it was not until after he retired

in 1989 that we were able to renew our friendship. At that time he asked me if I would identify some Geometridae that were in the Oakland Museum collection. I felt honored for this opportunity to return some of the help he had given me and for the trust he had in me.

After Don returned to the Cal Academy I would visit him as much as possible. As usual, he was always willing to take the time to show me his current project, identify some little thing for me, or we would talk of our families, past trips, or of the problems in the world of Lepidoptera.

Richard M. Brown

At UC Berkeley, Don was in Entomology and I was in Zoology, but—as fellow skipper fanciers—we had learned of each other's existence and had made contact by the end of my first year of graduate school (June 1955). Sarah and I quickly became close friends with Don and Grace, baby-sitting for them on occasion, and getting progressively absorbed into their welcoming family. We spent many an evening at their home, where Don and I often talked skippers and perused specimens for hours—though not to the exclusion of discourse on many and various unrelated topics or the tangential viewing of, say, Peter Gunn (a 1950s detective show with a music score by Henry Mancini; Sarah and I lacked television). Don was informative, thoughtful, generous, outgoing, meticulous, patient, and unassuming—with a fine sense of humor, to boot. He took me on a number of field trips in the San Francisco Bay Area, as much to demonstrate local ecology as to observe some specific population of *Hesperia*.

In mid-September 1955, Don drove Sarah and me down the Central Valley, over Tehachapi Pass, and through the Mohave Desert to what struck us easterners as the inaptly named New York Mountains to look for specimens of what Don in 1964 would formally describe as *Hesperia pahaska martini*. For Sarah and me this trip was an introduction to the expansive desert, as well as to some small heat- and drought-resistant ferns growing in rock crevices, to ascalaphids (owlflies) coursing low over a pale dirt road at dusk, and then, by Coleman lantern, to Don's wonderfully sustaining glop of variable and uncertain composition. In the course of just two days, we collectively amassed 63 males and 63 females of the energized and hard-flying skipper—which fortunately would nectar at times on low, scattered flowers induced by late summer rains. This was the sort of sample of a barely known differentiate that Don relished for assessing variation. Although the vintage car that carried the three of us to the desert and back was none too fond of the heat, it did not seem to bother Don: he went hatless and often shirtless. His remarkably broad shoulders were well tanned.

Amassing the type series of *Hesperia miriamae* was quite another matter. This skipper was only known to occur above timber line in the Sierra Nevada. Don directed his field attention to the vicinity of Mono Pass—approached from the eastern side of the Sierras—in northwestern Inyo County. Sarah and I accompanied him to that locality in mid-August 1956. Reaching the hostile skipper habitat required a switchback climb of several hours from the nearest permissible campsite. As luck would have it, a tiring hike begun on a beautiful cloudless morning might culminate at midday in a gray view of an overcast study area. On days when the sun did shine at 12,000 ft. and skippers were about, they were hard to pursue across the loose talus. When a cloud came over the sun, the temperature instantly plunged, and insect activity ceased. But more memorable than this difficult collecting was the automobile trip to and from the eastern slope of the Sierras. The road taken went over Sonora Pass. That road, though paved, was extremely narrow and winding and, in its upper reaches, steep—so steep, in fact, that Don's old car (one of a few he dubbed "The Wheezer") could not go up it even in first gear. Accordingly, on either side of the Sierras, at that dizzying point at which his car no longer advanced, Don, with total aplomb, would simply turn it around on the narrow mountain road, stick his head out the window, look backward, and proceed to drive over the pass in reverse at a speed close to what it had been when he was facing forward.

Sarah and I spent July 1974 (with our three children, ages 7 to 13) at the Southwestern Research Station in southeastern Arizona, where Don joined us for several days. On one of those, I drove him and my family from the Chiricahua Mountains to the Pinaleno Mountains in our new Volvo station wagon, which managed to go up all but one dirt road on the top of Mount Graham in first gear. Don was so taken with this vehicle that he soon got one for himself—and he stuck with that make for the rest of his life. We stopped to collect at various points along the crest of the Pinalenos. Already, our kids were calling him Paul Bunyan. He, Laura (our oldest), and I discussed the world in many of its nonentomological aspects as the rest of the family slept during our late night return through the lonely desert to the Chiricahuas.

When Don stayed with us in northern Virginia for a few weeks in May and June 1987, we took him skippering to the top of the Appalachians, from which we were driven by a torrential afternoon thunderstorm. Don loved it, despite the abrupt curtailment of field

work. Another day, Don stepped onto the open porch of our home to be as close as dryly possible to an intense thunderstorm. His fascination was almost childlike. We also took him skippering to the Carolina coastal plain. Although collecting was mostly good, he disliked the humid heat. He was a native Californian.

This human being, friend, and colleague—and his knowledge of skippers, natural history, and western ecology—will be sorely missed.

John M. Burns

I first met Don, as a freshman at UC Berkeley, when Jerry Powell suggested that I visit the California Academy of Sciences in Golden Gate Park and introduce myself to Don in the Entomology department. Don was warm and gracious, and immediately put me at ease by offering me a cup of coffee and directing me to the saturniid cases. If I were to be a regular visitor I knew I would have to pay my dues. At first I was excited at the prospect: "We have some saturniids that need some work." With that inducement, Don pulled out a drawer and with a revealing grin showed me row after row of drab, little *Hylesia*, a Mexican genus of saturniid unknown to me and virtually ignored, for obvious reason, by collectors. I managed a weak imitation of enthusiasm, but listened carefully as Don showed me the techniques of genitalia dissection and preparation. Apparently I passed this test of commitment, but certainly didn't contribute much to *Hylesia* taxonomy.

I began making routine Saturday trips to the Cal Academy, where Don introduced me to other lepidopterists, such as Bill Tilden, and a young man named Paul Opler. Don and I quickly became friends, in spite of our age difference. I was drawn to his sense of humor, lurking beneath his quiet demeanor, which often prompted Don to laugh at human folly in himself or in others. Don was modest, not a forceful public speaker, and not a self-promoter. He was intolerant of pompous authority, especially in bureaucrats, but respected good science, good writing, and a quick mind in those around him. In private discussion of his work, he would become serious and carefully choose his words and expressions. He was fair and generous in his dealings with others, which stemmed from a deep commitment to individual and civil rights.

I was soon invited to his house in the El Cerrito hills, where I met Grace, his daughters Lindy, the twins Daren and Nora, the cat and rabbit (who played together!), and pet Pacific giant salamander (which I thought was especially cool). I would make a half-hearted attempt to play basketball with Don and the girls, using a hoop over his garage. I was more effective at helping with his daughter's math homework, often ignoring Don's admonition to not give them the answer, but make them work for it. The MacNeill family was a home away from home for this college student from Iowa.

Don was proud of his lab over the garage, which housed his skipper collection. He introduced the *Hesperia* species almost as personal friends, each with its distinctive life history and distribution. He showed me how important it was to lay out a series of specimens in a pattern that reflected their geographic distribution, and in this way try to make sense of variation in terms of populations and gene flow. Don encouraged my interest in genetics and evolution and urged me to take G. Ledyard Stebbins's course in these subjects. Himself a product of the 'New Evolutionary Synthesis' of genetics, ecology and systematics, Don passed on to me his enthusiasm for the writings of Dobzhansky and for this multidisciplinary school of thought in evolutionary biology. Don's thesis work in *Hesperia* (MacNeill 1964) reflects his broad view of systematics and his attention to detail and clear writing.

After Don moved from the Cal Academy to the Oakland Museum he immediately immersed himself in helping plan the transect display and would proudly show me its progress whenever I visited. There may still be on display in the foothill case a "calling" female *Hyalophora euryalus* he asked me to donate. Outside of his skipper work this project was probably his most important contribution, the product of an immense amount of work.

On field trips together in the 1970s Don would take time out to collect one of his favorite ferns, usually a species fond of growing out of rock outcrops reached only by a difficult climb. I have a photograph of Don, I believe on Little Grey Back peak in the Trinity Alps, swinging his rock hammer, shirtless and enduring nasty bites from tabanids, yet with a big grin as he extracted one of his prizes. Camping and field trips with Don were truly seminars, a chance for Don to share his detailed and personal knowledge of California natural history.

One of my most favorite memories of time with Don goes back to June 1966 when we drove down US 395 and he introduced me to the east side of the Sierra Nevada with its magnificent vistas of sagebrush-covered slopes and massive rock formations. Earlier Jerry Powell had shown me a *Hyalophora gloveri* from near Bishop; I had not known it occurred west of Utah. Given their tendency to hybridize, Don and I predicted we might find hybrids between *gloveri* and *euryalus* somewhere on the east slope. We first camped near Tom's Place and I took my first California *gloveri*, attracted to a bred

cecropia female I had tied out. The next night as we made camp along the Walker River Don suggested we collect dead branches of Mountain Mahogany (*Cercocarpus*), whose dense wood makes a wonderful campfire. After a meal of beef stew with noodles referred to by Don as glop, he made "twisties" from Bisquik wrapped around willow branches, baked over the fire, and filled with jelly. Just before dawn the next morning the *cecropia* female attracted *gloveri*-like males but with the long hind wing eyespots of *euryalus*. We had found the eastern boundary of a population of hybrids. This trip eventually led, with Don's help and encouragement, to my thesis work with the hybrid zone across Monitor Pass, and for that and much more I owe a debt of gratitude for Don's friendship, companionship, and guidance.

Michael M. Collins

Don MacNeill was one of my important mentors during high school and my undergraduate years, and became a good friend and colleague after that period, in the 1950s and early 1960s. For me to remember specifics from that time is in the spirit of William Henry Hudson's remembrances of the Argentinean pampas in his book "Far Away and Long Ago."

Don was always ready to listen to young people with an interest in biology or entomology. I remember that about the only correspondence I had with Don was while I was in high school. I forget what the letter was about, but Don did return my letter with a complete reply. These letters are now in the historical archives of the California Academy of Sciences.

I think our first field venture was to Plantation in Sonoma County where Don was trying to discover the larval host of the population of *Pyrgus ruralis* that occurred there. I don't recall all of the participants but I think John Burns was also along on that trip. There was a lot of discussion as there always was with Don present. Don did a lot of his thinking out loud about potential hosts and how one could (maybe) discover a species host plant by following females in the field.

In 1957, after finding two sympatric and synchronic entities in the *Plebejus acmon* complex in Kern County, California, Don showed me how to dissect and study male genitalia of this group as I was preparing to give my first formal presentation to the Pacific Slope section of the Lepidopterists' Society in Santa Barbara at the end of the summer. (I'm still studying them and there has been no up-to-date revision of the group!)

The major trips that I remember with Don were 3-4 day expeditions in 1959 and 1960 to Mono Pass to search for anything that might be discovered about the life stages of *Hesperia miriamae* MacNeill, described in honor of his mother. Accompanied by the late Herman Real on both trips, we drove over Sonora Pass, drove south on U.S. 395 and camped at Tom's Place at the base of Rock Creek Canyon. Then, for two days, we would arise, cook breakfast, make our bag lunches, and drive to the end of the road, and park at 10,000 ft. We hiked the few miles and 3000 foot increase in altitude to Mono Pass where we searched, usually in vain, for the fabled *Hesperia*. In the process, I learned a lot about California alpine Lepidoptera—a small but distinctive lot. To this very day, the east side of the Sierra is one of my favorite places on Earth and one of the most intriguing.

In subsequent years, Don was always ready to give advice or make suggestions. My thoughts about butterfly behavior now center on Don's view of male mate-locating behavior. If one wishes to read some of the best writings on butterfly variation, behavior, and natural history, there is nothing better than to curl up on the couch and read his doctoral dissertation on the systematics of the genus *Hesperia*. It amazes me how precisely Don was able to express his findings. I also understand it was an experience not to be forgotten to have Don edit one's writings [Yes!—MMC].

Don is one of the finest people I'll have the pleasure of having known during my all-too-brief term on the planet.

Paul A. Opler

I first met Don MacNeill in September 1954, prior to my senior year at Berkeley, when I returned to campus early in order to attend the first meeting of the Pacific Slope Section of the Lepidopterists' Society, in San Francisco. There a lifelong association with several lepidopterists began, and I learned that Don would be the Teaching Assistant in R. L. Usinger's Systematic Entomology class that fall. The lab dealt with methods and literature, and Don was the instructor. We were shown a bunch of specimens and asked to select one for some exercises, so naturally I selected the largest one, figuring it would be the easiest to identify, which pretty much had been the extent of my experience in taxonomy. I picked a tarantula hawk; I imagine Don just smiled. The following weeks, when we students had to locate the original description, the location of the type specimen, citations for the synonyms, who proposed the synonymies and when and so on, I absorbed my first lesson from Don—trophy insects were described a long time ago, usually in obscure, difficult to locate literature, and often have nomenclatural problems. Later we wrote diagnoses, descriptions, keys to a small group of species

of our choice, and somehow my choice was skippers, *Pholisora*. It was the first time I had looked at Lepidoptera under a scope and tried to locate differentiating characters. In the margins of the exercises Don began to bring me up to speed, writing comments such as "did you look at x, y, or z structures?" or "these two couplets do not compare the same characters."

In the spring of my senior year I worked part time in the museum and sometimes lunched with Don and other graduate students, where I heard tales of futile search for ancient types, responses from butterfly collectors in the east or Colorado who would not loan specimens to Californians for fear of earthquakes, or other lame excuses, and hurdles posed by inactive self-appointed specialists. A picture of my future research direction gradually came into focus—steer clear of macroleps, especially butterflies. During my first year or two in graduate school, Don was making weekly or bi-weekly trips to Marin County for *Hesperia* life history studies. I tagged along, and we rode the ferry across the bay, which involved coffee upstairs and discussions of biogeography, whether territoriality is a concept applicable to butterflies, and other questions that came to mind. Most memorable, however, are images of Don in his Air Force fatigue jacket crouching in cold, blowing fog checking the status of eggs of *H. lindseyi* laid on lichens on fence posts, and searching on hands and knees for eggs and larvae of *Pyrgus scriptura* on alkali mallow in the Sacramento Valley in November, when it was finger-numbing 40° and dripping wet from the tule fogs. I realized that life history studies do not just happen while you are cavorting in sunny meadows in the spring. His dedication to documenting the behavior and early stages was never more evident than in 1957 when one day we climbed Sonora Peak, 11,500 ft. and each of the next five days hiked from 9,700 ft. to Mono Pass above 12,000 ft., in search of the elusive female of *H. meriamae*, from whom he wanted to obtain eggs. At Mono Pass, the diurnal moths *Orenaia macneilli* and the remarkable *Epiblema macneilli*, which most closely resembles a Siberian species, were among the many discoveries he made in subsequent years.

By 1961 we had our respective positions in San Francisco and Berkeley, our futures seemed intertwined, and Don conceived the idea of making a series of weekly trips to the foothills of the Sierra Nevada, gradually working our way upward as the season progressed, simply because collectors routinely drove past lower elevation places on their way to the high Sierra. We began in April, and on our first visit I collected larvae of *Ethmia plagiobothrae*, a widespread moth nobody had seen until the first adult emerged the following February. We visited sites as available, rather than because other collectors had, and a strategy of selecting areas to work based on geographic and seasonal gaps in the record was adopted as the approach for the California Insect Survey during the subsequent 20 years. In 1972 we made a memorable expedition to the Sierra Madre Occidental in Sinaloa and Durango with Don Veirs and collected *Carollella macneilli*, in addition to successful pursuits with our own interests. But after Don took the position at the Oakland Museum, we spent less time together. He was generous with his time when contacted, but in retrospect, I believe he relied upon others' initiative for social and professional contact. As our commitments broadened, the frequency of my calls waned. I do not recall him ever visiting the Essig Museum of his own accord, before or after retirement. I imagine him now in the Big Museum in the Sky, smiling tolerantly at our musings about his life.

I doubt that Don was aware of his lasting influence on me during those early years—moderation of initial impulses, reasoned discussion of ideas, a dedication to integrating behavior and biology with classical systematics, persistence and patience (though some might argue the last failed to take), but also, inadvertently, not endless patience because the puzzle is never completed in biology, so there is a need to recognize when a project should be closed.

Jerry A. Powell

I met Don MacNeill at the August 1991 Lepidopterists' Society meeting in Tucson, Arizona. We talked for about thirty minutes and had a good exchange of interests which led him to invite me to visit him at the California Academy of Science in San Francisco. I accepted and spent several hours there on December 3, 1991, and discussed possible field trips during the next season.

During the next years we went on many collecting trips. Our first was to Del Norte County, California, and Jackson County, Oregon, from June 16 through 19, 1992.

The high point of this trip was finding *Polites mardon* at both locations. During this first trip we discovered not only a shared interest in skippers and field trips, but also that we both enjoyed tasting a little red wine each evening. In fact, these interests inspired him to say we were compatible traveling companions.

I never got to know much about his personal life and very little about details of his life history. His comment to me during the first trip or so was "I really don't care for small talk." That comment cut out most of our

conversations to the extent we would travel many miles without saying anything other than "where do you want to eat?" or "we better have a rest stop."

We attended the Pacific Slope meeting in July 2002 at Camp Keep, Tulare County, California. After the meeting we drove to Big Pine, California, and on to the Bristlecone Pine Forest in the White Mountains. We parked at the base of the 11,543 ft. Campito Peak. Don wanted to hike to the top to look for *Hesperia miriamae*, but it was apparent after a short steep walk that he couldn't go any higher. I decided to go on alone to the top. I saw small brown skippers there but they were all *Hesperia comma* and *Polites sabuleti*.

Don, then seventy-seven years old, decided he wanted to come back the next day, after he was acclimated to the high elevation, to hike up Sheep Peak, not far from Campito, but higher (12,497 ft.). Sheep Peak turned out to be a long, steep, one mile walk from the road. The last quarter mile or so was very steep. Don was determined to go to the summit, so he would stop every few minutes and take a pill. I asked about the pills and he said they were nitroglycerin for his heart and he was afraid he was going to run out before we got to the top. Of course I was horrified because if he passed out I would never get him back to the car. Being a tough old bird he made it. This was all in vain since there were no *miriamae*.

The last trip was in October 2004 to southeast Arizona to look for *Adopaeoides prittwitzi*. This is a small skipper, rarely found near the Mexican border in wet areas. Unfortunately we found none due to extremely arid conditions at the time.

All our trips were mainly in search of the various species and subspecies of *Polites* and *Hesperia*. Don was collecting information to determine which species and subspecies deposited eggs by sticking them on food plants or by dropping them on the ground around or near the food plant. He would collect live females (he called them his ladies), put them in vented jars with food plants and observe which method they used for depositing their eggs. We made at least twenty trips which covered many parts of California, Nevada, Utah, Oregon and Arizona. Each trip lasted four to ten days. We attended Pacific Slope meetings in July 1996 at Ephraim, Utah, and in July 2002 at Camp Keep, Tulare County, California.

John Vernon

ENTOMOLOGICAL PUBLICATIONS BY C.D. MACNEILL

ADAMS, P. A. AND MACNEILL, C. D. 1951. *Gelastocoris rotundatus* Champion in California (Hemiptera: Gelastocoridae). Pan-Pacific Entomol. 27: 71

MACNEILL, C. D. 1957. Book Review: The Butterflies of the Malay Peninsula, by A. S. Corbet and H. M. Pendlebury. Pan-Pacific Entomol. 33: 96-99.

ROZEN, J.G. AND C. D. MACNEILL 1957. Biological observations on *Exomolopsis* (*Anthophorula*) *chionura* Cockerell, including a comparison of the biology of *Exomolopsis* with other anthophporid groups (Hymenoptera: Apoidea). Ann. Entomol. Soc. Amer. 50: 522-529.

MACNEILL, C. D. 1959. A new species of *Hesperia* from California (Lepidoptera: Hesperiidae). Wasmann J. Biol. 17: 89-94.

MACNEILL, C. D. 1961. Book Review: How to Know the Butterflies, by P. R. and A. H. Ehrlich. Pan-Pacific Entomol. 37: 135-136.

MACNEILL, C. D. 1962. Notes on the flight behavior of *Ulolodes* sp. (Neuroptera: Ascalaphidae). Pan-Pacific Entomol. 38: 186-188.

MACNEILL, C. D. 1962. Preliminary report on the Hesperiidae of Baja California (Lepidoptera: Hesperiidae). Proc. Calif. Acad. Sci., 4th Series 30: 91-116.

MACNEILL, C. D. 1962. Observations on the voluntary display of coremata in *Estigmene acrea* (Lepidoptera: Arctiidae). Pan-Pacific Entomol. 38: 195-198.

MACNEILL, C. D. 1963. *Callophrys fotis* Strecker at San Bruno Mountain (Lepidoptera: Lycaenidae). In: Proc. Pac. Coast Entomol. Soc., 279th Meet. Pan-Pacific Entomol.39: 60.

MACNEILL, C. D. 1964. The skippers of the genus *Hesperia* in western North America, with special reference to California (Lepidoptera: Hesperiidae). U. Calif. Publ. Entomol. 35; 230 pp.

MACNEILL, C. D. 1967. A unidirectional mass movement by *Satyrium saepium* (Lycaenidae). J. Lepid. Soc. 21: 204.

MILLER, L. D. AND C. D. MACNEILL 1969. Reports on the Margaret M. Cary-Carnegie Museum Expedition to Baja California, Mexico, 1961. 5. Two new subspecies of Hesperiidae (Lepidoptera) from the Cape Region, Baja California Sur, Mexico (Lepidoptera). Ann. Carnegie Mus. 41: 19-24.

MACNEILL, C. D. 1970. A new species of *Pholisora*, with notes on *P. alpheus* Edw. (Lepid.: Hesperiidae). Entomol. News 81: 177-184.

MACNEILL, C. D. 1975. Family Hesperiidae, The Skippers. pp. 423-578 in: Howe, W. H. (ed.). The Butterflies of North America. Doubleday & Co., Garden City, NY.

ARNAUD, P H. JR. AND C. D. MACNEILL 1988. In Memoriam. Pedro W. Wygodzinsky, 1916-1987. Pan-Pacific Entomol. 64: 297-298.

HERRRERA, J., C. D. MACNEILL, AND J. ATRIA 1991. Revision taxonomica del Genero *Butleria* (Lepidoptera: Hesperiidae). Acta Entomol. Chilena 16: 201-246.

MACNEILL, C. D. 1992. Obituary. José Valentítin Herrera González (1913-1992). J. Lepid. Soc. 46: 248-254.

MACNEILL, C. D. 1993. Comments on the genus *Polites*, with the description of a new species of the *themistocles* group from Mexico (Hesperiidae: Hesperiinae). J. Lepid. Soc. 47: 188-198.

MACNEILL, C. D. AND J. HERRERA G. 1998. Studies in the genus *Hylephila* Billberg, I. Introduction and the *ignorans* and *venusta* species groups (Hesperiidae: Hesperiinae). J. Lepid. Soc. 52: 277-317.

MACNEILL, C. D. 2002. Studies in the genus *Hylephila* Billberg, II. The *boulleti* species group (Hesperiidae: Hesperiinae). J. Lepid. Soc. 56: 66-89.

TAXA OF HESPERIIDAE DESCRIBED BY C. D. MACNEILL:

Hesperia miriamae MacNeill, 1959
Hesperia pahaska martini MacNeill, 1964
Hesperia uncas gilberti MacNeill, 1964
Hesperia uncas macswaini MacNeill, 1964
Cogia hippalus peninsularis L. Miller and C. D. MacNeill, 1969
Polites sabulatis margaretae L. Miller and C. D. MacNeill, 1969
Pholisora gracielae MacNeill, 1970
Nivis Herrera, MacNeill, and Atria, 1991 (subgenus of *Butleria*)
Marthae Herrera, MacNeill, and Atria, 1991 (subgenus of *Butleria*)
Polites norae MacNeill, 1993
Hylephila adriennae MacNeill & Herrera, 1999
Hylephila lamasi MacNeill & Herrera, 1999
Hylephila kenhaywardi MacNeill, 1999 [new name for *H. haywardi* (Ureta), a homonym]

Hylephila blancasi MacNeill, 2002
Hylephila herrerai MacNeill, 2002
Hylephila pseudoherrerai MacNeill, 2002
Hylephila pallisteri MacNeill, 2002
Hylephila rossi MacNeill, 2002
Hylephila shapiroi MacNeill, 2002
Hylephila tentativa MacNeill, 2002

PATRONYMS

Orthoptera
Neduba macneilli Rentz and Birchim, 1968 (Tettigoniidae)
Coleoptera
Oropus macneilli Schuster and Grigarick, 1960 (Staphylinidae)
Diptera
Telmatoscopus macneilli Quate, 1955 (Psychodidae)
Agathomyia macneilli Kessel, 1961 (Platypezidae)
Hymenoptera
Pseudomasaris macneilli Bohart, 1963 (Vespidae)
Lepidoptera
Ethmia macneilli Powell, 1973 (Ethmiidae)
Orenaia macneilli Munroe, 1974 (Crambidae)
Epiblema macneilli Powell, 1975 (Tortricidae)
Carolella macneilli Razowski, 1986 (Tortricidae)
Poanes macneilli Burns, 1992 (Hesperiidae)
Schinia macneilli Hardwick, 1996 (Noctuidae)
Hesperia lindseyi macneilli Emmel, Emmel, and Matoon, 1998 (Hesperiidae)

We greatly appreciate assistance of Grace MacNeill, Don's ex wife and lifetime friend, in providing personal details and compiling additions to his bibliography.

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LEPIDOPTERA OF FLORIDA PART 1 INTRODUCTION AND CATALOG, by John B. Heppner. 2003. Florida Department of Agriculture & Consumer Services, Gainesville, Florida. 670 p. ISSN: 0066-8036. Available for $45.00 for the spiral bound edition and $55.00 for perfect bound version. Order from Publications, DPI Technical Assistance. P. O. Box14711, Gainesville, Florida 32614 US.

The State of Florida's influence on knowledge of Lepidoptera in the United States is steeped in history and interest. John Abbot's beautiful paintings, the basis of Smith and Abbot's *The natural history of the rarer lepidopterous insects of Georgia: Including their systematic characters, the particulars of their several metamorphoses, and the plants on which they feed / Collected from the observations of Mr John Abbot, many years resident in that country* (1797), illustrated species from Georgia many of which are found in northern Florida. Several papers described species known only from Florida, and J. A. Grossbeck's *Insects of Florida. IV. Lepidoptera* (1917) gave an early look at a Florida statewide list. Until recently, the single most important contribution to knowledge of Florida's lepidopteran fauna was Charles P. Kimball's *Arthropods of Florida and Neighboring land areas, Volume 1. Lepidoptera of Florida* (1965) which originally sold for the incredibly low price of $5.00 when published in 1965. Two, of many, more important contributions came from Baggett (1982) and Dickle (1991). Keen interest in Florida's fauna attracts many collectors and observers, and an update to Kimball's book was in demand.

Enter the long awaited *Lepidoptera of Florida Part 1 Introduction and Catalog* (Heppner, 2003). I had the opportunity of providing a reviewer's look at a draft manuscript, and I'm pleased to write this review of the published book. Without hesitation, I like this book, and it seems required literature in understanding Florida's fauna. The book doesn't come without detractors because of a couple of perceived shortcomings—most understandably the lack of color plates. I want color plates, but I don't want to pay the very high associated publication costs to produce 55 color plates. Heppner also uses his classification scheme (1998) which is not in total agreement with other more widely accepted views (Kristensen, 1998). I find both of these concerns to be minor details, mentioned so the reader knows what to expect.

We generally understand that the distribution and abundance of Lepidoptera are products of phytogeography, geology, climate, soils, and a host of other factors generally termed biogeography. What happens in Florida is no exception—its unique nature comes from its tropical southern tip, its remnants of northern fauna from the influence of the Appalachian Mountains in northern Georgia, its relative flat relief, and its Gulf coastal environs which directly connect Florida to western habitats seen in Texas. Heppner begins this book with a discussion of these factors. His maps illustrate Florida's biogeography and they, along with the accompanying text, give a concise overview of the state's regions, which are important elements to understanding lepidopteran distribution in the state. Heppner related these factors to distributional tendencies. Heppner provided a gazetteer to locate specific sites within the state's biogeographic region. Florida's geographic location and factors which make it unique create conditions conducive to endemic species, and these are highlighted by Heppner.

The text provides an overview of the study of Lepidoptera with specific emphasis on Florida. Topics include collecting, curating, rearing, and other techniques. The morphology of Lepidoptera is illustrated with line drawings. The next several pages are lists of families of Lepidoptera by scientific name, the classification scheme used in this work, common name, a table of numbers of species by family and genus, and name changes since Kimball (1965). The keys to families are written on a scheme based on 8 major divisions of families based on morphological features, such as "Microlepidoptera with scaled haustella," "Butterflies and butterfly-like moths," "Noctuoidea," and others. The morphological features used in the keys require sophistication, and for a novice user, they will be frustrating. For example, couplet 3 in the Key to Sections requires knowledge of presence or absence of a tympanal organ. Without a knowledge of all the possible locations of the tympanal organ, the user will be stumped. For a more experienced user, the keys highlight discriminating features at the family level, and in that way, the keys are useful.

Pages 119 through 227 are 55 black and white plates of adult Lepidoptera. The plates are excellent, and they are not in color. The cost of producing a book of this size (670 pages) with 55 color plates would be prohibitively expensive to purchase. As much as I like color plates, these photos are excellent for elucidating the general habitus of the species which are illustrated. Other literature should always be employed for difficult identifications. I would have preferred that the species be illustrated in checklist order, so that all species within a related group are adjacent to each other on the plates.

For example, my use of the plates to find illustrations of Zygaenoidea (*sensu* Epstein *et al.*, 1998) required that I search 3 widely separated plates whereas 1 plate would have been sufficient. Heppner used plates from Kimball (1965), and he included several additional plates for species not illustrated in Kimball.

Pages 231–484 contain the "Catalogue of Florida Lepidoptera." The catalogue format is explained and the catalogue is presented in Heppner's systematic order. Information includes classification, the Hodges (Hodges *et al.*, 1983) Check List number, the McDunnough (McDunnough, 1939) Check List number if available, and author and year (the original combination is not presented). If no Hodges Check List number is available, a new number is coined. The catalogue also includes annotations for each species; the distribution in Florida (by Florida biogeographic region), the distribution in the United States, the months of collection in Florida, and larval hosts when known. For each species which is illustrated in the 55 plates, a direct reference to the illustration is given.

The text continues with "References," which is a bibliography of Florida references. A "Hostplant Index," lists host plants in alphabetical order by plant genus. The lepidopteran species using each host plant are listed by lepidopteran check list number. Common names of plants, also in alphabetical order, provide a cross reference to the plant scientific name. Three indices for the animal names, species, genus, and common name complete the book. The species and common name indices use lepidopteran check list numbers, and the genus name index uses page number to locate entries.

Other compilations in this work are lists of species in the categories of Exotic Lepidoptera, Lepidoptera Pests in Florida, and Pest Name Index, Stray Lepidoptera in Florida, Beneficial Lepidoptera in Florida, and Erroneous Florida Lepidoptera Records.

The construction of the book is inelegant. The buyer is given a choice of two bindings; plastic comb or perfect binding (in which the pages are glued together along the inside margin). Neither binding is very good, and they will not last for long. My copy (plastic comb) was apparently run off on a photocopy machine, and black streaks (often found on photocopies made from a machine in need of maintenance) grace the bottom margin of many of the pages. The unnecessary blemish of the streaks portrays inadequate quality control.

No book is perfect nor does any book provide everything that all readers want. Some books come closer than others, and this book is right on target. For my needs, this book is an important document, and it is excellent. For lepidopterists with any interest in Florida, this book must be part of their accumulated information. For naturalists needing a quick read on Florida's biogeography, this book should be useful. I cannot image continuing my lepidopteran studies without this book. I cannot imagine continuing my lepidopteran studies by relying on only one source of information. I've already used this book for research; it gave me the data I needed. I will use this book again and again.

LITERATURE CITED

BAGGETT, HOWARD DAVID. 1982. Lepidoptera (p. 72–81) in Rare and Endangered Biota of Florida, Vol. 6, Invertebrates. (R. Franz, Editor). University Presses of Florida, Gainesville, Florida. 131 p.

EPSTEIN, MARC E., HENK GEERTSEMA, CLAS M. NAUMANN, AND GERHARD M. TARMANN. 1998. The Zygaenoidea (p. 159–180). *In* Handbook of Zoology, Volume IV Arthropoda: Insecta, Part 35, Lepidoptera, Moths and Butterflies, Volume 1: Evolution, Systematics, and Biogeography. Niels P. Kristensen (editor). Walter de Gruyter, Berlin, Germany. "1999" 491 p.

GROSSBECK, J. A. 1917. Insects of Florida. IV. Lepidoptera. Bulletin American Museum of Natural History 37(1): 1–147.

HEPPNER, JOHN B. 1998. (Classification of Lepidoptera part 1. Introduction. Holarctic Lepidoptera. 5(suppl. 1): 1–148.

HEPPNER, JOHN B. 2003. Lepidoptera of Florida Part 1 Introduction and Catalog. Florida Department of Agriculture & Consumer Services, Gainesville, Florida. 670 p.

HODGES, RONALD W., TATIANA DOMINICK, DONALD R. DAVIS, DOUGLAS C. FERGUSON, JOHN G. FRANCLEMONT, EUGENE G. MUNROE AND JERRY A. POWELL. 1983. Check List of the Lepidoptera of America North of Mexico including Greenland. E. W. Classey Ltd. & The Wedge Entomological Research Foundation. London, England. 284 p.

KIMBALL, CHARLES P. 1965. Arthropods of Florida and Neighboring land areas, Volume 1. Lepidoptera of Florida. Florida Department of Agriculture, Gainesville, Florida. 362 p.

KRISTENSEN, NIELS P. (editor). 1998. Handbook of Zoology, volume IV Arthropoda: Insecta, part 35, Lepidoptera, moths and butterflies, volume 1: evolution, systematics, and biogeography. Walter de Gruyter, Berlin, Germany. "1999" 491 p.

MCDUNNOUGH, JAMES HALLIDAY. 1939. Check List of the Lepidoptera of Canada and the United States of America. Part II, Microlepidoptera. Bulletin Southern California Academy Sciences Vol. II: 1–171.

SMITH, J. E. and John Abbot. 1797. The natural history of the rarer lepidopterous insects of Georgia: Including their systematic characters, the particulars of their several metamorphoses, and the plants on which they feed / Collected from the observations of Mr John Abbot, many years resident in that country. London : Printed by T. Bensley, for J. Edwards. 2 volumes (100 p., 50 plates; p. 101–214, plates 51–104).

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THE MOTHS OF NORTH AMERICA INCLUDING GREENLAND. FASCICLE 15.5 PYRALOIDEA, PYRALIDAE (PART), PHYCITINAE (PART) by H. H. Neunzig, 2003. (ed. R. W. Hodges) Softcover, ISBN: 0933003110. Publisher: Wedge Entomological Research. Distributed in the USA by Entomological Reprint Specialists, Los Angeles CA. Softcover, price: $115.00 plus $4.00 shipping/handling [USA, Canada, Mexico], $5.00 shipping/handling [elsewhere].

Representing the fourth fascicle on the North American Phycitinae, this book deals with a larger assemblage of genera and species than the preceeding three. Neunzig states, as in previous fascicles, that there is still insufficient phylogenetic evidence to confirm natural groupings of genera within the subfamily and expressed the opinion that, based on our knowledge of the subfamily, it is premature to attempt a tribal classification. The genera dealt with in all the fascicles are grouped for ease of identification and defers from a phylogentic arrangement. Though Neunzig's work is restricted to covering the fauna of North America, including Greenland, it of course greatly exceeds the number of taxa dealt with in this region by Henrich (1956.U.S.N.M. Bull. 207), who in addition dealt with South and Central America. The updated works of Neunzig now naturally supplant Heinrich's pioneering volume, though the basic classification has not altered.

The research involved in this fascicle included exhaustive tracking of type material to ensure accuracy of identifications, plus examination of much additional material from collections all over the U.S.A. and Canada. This helped to ensure adequate material for study and importantly, allowed for coverage and understanding of geographical variation. Forty-seven genera are treated, covering 218 species, which include several new generic taxa and numbers of new specific taxa. In addition, many new combinations are established. The work is divided into major groups of genera, with each group preceeded by general descriptive notes, plus detailed keys to the identification of genera. Each genus is adequately described and notes on larvae and pupae are included when they are known. Keys are provided for species within each genus. For every species a brief discussion along with descriptive remarks are accompanied by the species original combination and reference, location and depository of type material, information on larval food plants, geographic distribution of known material and most importantly, text figures of male and female genitalia, plus colour photographs of the adult moth. Special attention is given to the prolific and important genus *Dioryctria*, the species of which are all associated with conifers. Table 1 lists the species, their known range of larval host plants and their distribution. This is an equally important and prolific genus through most of the Palaearctic and Asia.

A detailed bibliography is provided, also a checklist of the species covered, a general index, plus a very essential index to plants and fungus names mentioned in the text. Of special importance, excellent high powered monochrome photographs arranged as a group of plates are provided showing male antennae structures, essential in aiding the recognition of Phycitinae and possibly serving as an aid in formulating a methodology in their classification.

Apart from the high quality of the adult photographs, commendably, effort was made to use specimens in good condition and properly set, an aspect all too often sadly neglected in publications today, especially on Phycitinae. Commendable also is the high standard of the line drawings for genitalia, wing venations, antennae and larval instars, an aspect in scientific entomological literature which all too often can be shabbily treated, as can be seen from many works of Phycitinae over the years.

With the clear amount of effort put into the production of this fascicle, it is difficult to see why the color plates are somewhat marred by the fact that species of *Dioryctria*, which form the largest genus, are not kept together on plates 6 and 7, without a few trailing off to plate 8 and a few incorporated on plate 3; this same problem occurs for the genus *Sciota*. For comparison purposes it would have been more useful if species of a given genus were grouped consecutively.

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THE MOTHS OF NORTH AMERICA INCLUDING GREENLAND. FASCICLE 27.1: NOCTUOIDEA, NOCTUIDAE (PART): NOCTUINAE, AGROTINI, by J. Donald Lafontaine. 2004. (Ed. R.W. Hodges) 385 pages, 12 colour and 63 B&W plates, 136 text figures (1 phylogenetic tree and 135 maps), 21.5 x 27.8cm, ISBN 0-933003-12-9. Published by The Wedge Entomological Research Foundation, Washington, D.C. Distributed in the USA by Entomological Reprint Specialists, Los Angeles CA. Softcover, price: $115.00 plus $4.00 shipping/handling [USA, Canada, Mexico], $5.00 shipping/handling [elsewhere].

This is the third in a series of four MONA fascicles that together will revise all 540 species (currently) of Noctuinae found in Greenland, Canada, the continental United States and Mexico. The first to be published, fascicle 27(2) (Lafontaine, 1987), treated 171 species of the genus *Euxoa* (tribe Agrotini) found north of Mexico (three Mexican and one Costa Rican species were excluded). Next came fascicle 27(3) (Lafontaine, 1998), which dealt with the 169 species (31 genera) of tribe Noctuini, and extended the geographical area to include three species from northern Mexico. The present fascicle includes 181 species in the remaining 14 genera of Agrotini, of which 44 species are found only in Mexico, together with *Crassivesica*, here placed as a subgenus of *Euxoa*. This gradual expansion in geographical inclusiveness is also reflected in a subtle change to the title of the series, from The moths of America north of Mexico to The moths of North America. The fourth and final fascicle will complete the revision by treating an additional 19 species of *Euxoa* and presenting distribution dot maps of all *Euxoa* species, these having not been included in 27(2).

Fascicle 27(1) follows what has become the standard format for MONA. It opens with a general description of the structural features and biology of the tribe Agrotini. They are characterized as inhabiting primarily in open, xeric habitats and are usually the dominant group of Lepidoptera in deserts and grasslands, in contrast to Noctuini, which are mostly inhabitants of temperate forests. There follows an historical review of the taxa Noctuinae and Agrotini, tracing the groups from their origins in the mid-1800s through to the present day. In so doing, the author argues (rightly in my opinion) for retaining the traditional usage of subfamily Noctuinae, rather than the broader and more ill-defined concept that would incorporate such groups as Hadeninae, Cuculliinae (part) and Amphipyrinae (part).

The section on classification and distribution of Agrotini is co-authored with the eminent Danish noctuidologist, Michael Fibiger. They begin by describing the characteristics of the two tribes, Noctuini and Agrotini, emphasizing the apomorphic (derived) features that demonstrate the reciprocally monophyletic nature of each group. The third tribe of Franclemont & Todd (1983), "Aniclini", is rejected as a non-natural assemblage of lineages that simply lack many (but not all) of the derived characters typical of the other two tribes; the genera included in "Aniclini" have been reassigned to either Noctuini or Agrotini. Agrotini is divided into two subtribes. Australandesiina is a primarily South American group that is represented in North America by *Peridroma*, *Neodroma* (a new genus proposed for *Agrotis semidolens* Walker, a neotropical species that reaches central Veracruz in Mexico), *Anicla* (including subgenus *Euagrotis*), *Praina* and *Hemieuxoa*. The remaining ten genera (including *Euxoa*) comprise the subtribe Agrotina. A phylogeny of Agrotina genera is presented, including a cladogram, but synapomorphies are not shown mapped onto it. Instead, a narrative style is adopted, and unlike the discussion of the two tribes, synapomorphies are not emboldened. This makes it quite difficult to determine which are the symplesiomorphies and which are the synapomorphies, and what are their distributions among the various groups. It also leads to a certain laxness in argumentation in places, so that in the discussion of the interrelationships of *Richia*, we are told they "do not have character states to further group two of them into a monophyletic unit". Instead they are "arranged in a sequence based on 1) loss of the digitus on the valve, 2) reduction and change in orientation of the clasper, and 3) and [sic] increasing granular texture of the larval integument". However, just what aspects of these trends serve to group *Copablepharon* + *Protogygia*, and *Euxoa* + *Feltia* + *Agrotis* together to the exclusion of *Richia* are not stated.

Next follows a detailed description and discussion of the author's personal style of genital dissection. This will be very useful to many lepidopterists, especially those who are not already familiar with the procedures. The author also explains his preferred terminology for various genital structures, and pays particular attention to the vexed concepts of clasper, harpe and ampulla. While I appreciate the author's position, and accept that it differs from my own terminology, the grounds for confusion remain fertile. Maybe the time has come to determine a standard terminology for the main

lepidopteran genital structures, one that is more in line with those employed in other insect groups. Then, if valve has to give way to gonopod, aedeagus to phallus, and vesica to endotheca (Kristensen, 2003), so be it. Or is the historical contingency simply too great?

The remainder of the fascicle follows the now familiar style of the MONA series and is produced to the very high standards of this author. There is a key to genera based on adult features and one to mature larvae (co-authored with Suzanne Allyson). The latter, which includes only 34 of the 181 species treated in the fascicle, shows just how little is yet known of the immature stages of these moths. Under each genus are provided details of the original description, type species, synonymy, diagnostic features, a detailed head-to-tail description and a key to species (if two or more species are included). Under each species are a full synonymy (with explanatory notes), diagnostic features of adults and larvae (if known), distribution and a dot map. The label data used to generate these maps are stated to be available on-line at the web site for The Wedge Entomological Foundation. However, no URL is given and while a "Google search" on "The Wedge Entomological Research Foundation" on 23 June 2005 produced 135 hits, the data label site was not among them. In common with many other lepidopterists (myself included), the author has eschewed the requirement to make specific names agree in gender with that of the genus in which they are included. This really is an irrelevant diversion in 21st Century systematics that should have been eliminated from the nomenclatural code long ago (and apparently almost was last time round).

There are over 100 pages of monochrome and colour illustrations. There are explanatory guides to terminology of venation, wing pattern, adult and larval features, which perhaps could have been better cross-referenced in the main text. There are 52 monochrome plates illustrating male and female genitalia. These are generally well reproduced but a few are slightly out-of-focus and the contrast could have been higher on some. An interesting alternative format would also have been to have the males and females on facing pages, so that the morphological match between the two could be appreciated. However, I accept that this may not be to everyone's taste and would probably increase the size of the work, with associated financial implications for both the author and purchaser. The color plates are excellent and the use of a pale blue background is especially effective with the pale *Copablepharon* species.

The fascicle concludes with a list of institutional abbreviations, a checklist and indexes to moth and plant names.

Overall, this is yet another excellent contribution to both the MONA series and to noctuid systematics.

LITERATURE CITED

FRANCLEONT, J.G. & TODD, E.L. 1983. Noctuidae. Pp. 120-159, in Hodges, R.W. et al., Check list of the Lepidoptera of America north of Mexico, xxiv + 284pp. London: E.W. Classey Ltd and the Wedge Entomological Research Foundation.

KRISTENTSEN, N.P. 2003. Skeleton and muscles: adults. Pp. 39-131, in Kristensen, N.P., Handbuch der Zoologie 4 (Arthropoda), (2) (Insecta), (35) Lepidoptera. Moths and butterflies 2 (Morphology, physiology, and development), xii + 564pp. Berlin: Walter de Gruyter.

LAFONTAINE, J.D. 1987. Noctuoidea Noctuidae (part) Noctuinae (part - Euxoa). In Dominick, R.B. et al., The moths of America north of Mexico, fasc. 27.2: 1-237. Washington: The Wedge Entomological Research Foundation.

LAFONTAINE, J.D. 1998. Noctuoidea Noctuidae (part) Noctuinae (part - Noctuini). In Dominick, R.B. et al., The moths of America north of Mexico, fasc. 27.3: 1-348. Washington: The Wedge Entomological Research Foundation.

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